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ASPEN FORESTS OF JASPER AND BANFF NATIONAL PARKS

BY

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A THESIS

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Aspen Forests of Jasper and Banff National Parks" submitted by Phillip D. Lulman in partial fulfillment of the requirement for the degree of Master of Science.

ABSTRACT

Twenty-five stands of aspen *(Populus tremuloides var. aurea)* dominated forest were studied in the Front and Main Ranges of Jasper and Banff National Parks. Stands were distributed over broad elevational and moisture conditions. Soils were mainly Orthic Eutric Brunisols.

Based upon a Bray and Curtis ordination using Beals' species prominence values three community types were recognized: *Elymus innovatus*, *Shepherdia canadensis/Aster conspicuus* and *Vicia americana*. The community types were further subdivided into two groups representing a spectrum of site moisture regimes.

Community types are best defined by elevational differences and soil silt plus clay content. Differences between stands within each community are dependent upon available soil moisture and silt plus clay content, in addition to differences in degree and mode of moisture recharge.

Other studies demonstrate the climax nature of aspen forests in Colorado and Utah, but the unstable (subclimax) state throughout other areas. Jasper and Banff stands are considered subclimax.

Aspen in Jasper and in Banff is not regenerating rapidly, nor are successional conifer species prominent in the understory. Evidence from the stands studied suggests that white spruce is the most common species regenerating under aspen stands. The driest stands where little regeneration is evident may die out to provide an open shrub phase, unless fire stimulates aspen to regenerate by suckering. More mesic sites may persist longer and provide conditions for spruce succession.

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INTRODUCTION

The study of *Populus tremuloides* Michx. has historically concerned the forester and silviculturist. Seventy years ago aspen was looked upon as a forest weed to be replaced with more remunerative needle leafed evergreen species (Graham *et al*. 1963). An early treatise (Weigle and Frothingham 1911) summarized much of what was then known of the ecology of aspen.

Logging associated with frequent fire during the early part of the 20th century created conditions in many forested areas of northeast and northwest North America conducive to replacement of conifers with successional species, especially aspen (Clements 1910; Baker 1918). Subsequently, with so much aspen wood available, publications emphasizing management and utilization of aspen timber appeared more frequently (Baker 1925; Chase 1947; Stoeckeler 1948).

The importance of site quality or potential productivity to the growth of aspen is recognized in reports of Kittredge and Gevorkiantz (1929), Robinove and Horton (1928) and Stoeckeler (1948). Site quality was considered strongly dependent upon the soil silt plus clay content, a feature directly related to soil moisture and nutrient retention. Soil reaction was found to be best for aspen growth when slightly alkaline. Frequent fires are described as detrimental to site quality primarily as a result of the consumption of the upper organic layers of the soil.

In the past forty years there has been a steady increase in the

volume of literature dealing with aspen as an economic crop (Johnson *et al.* 1930; Chase 1947). Since a major portion of aspen regeneration is by adventitious shoots resulting in clones much attention has been paid to this mode of reproduction (Sandberg *et al.* 1953). Horton and Hopkins (1965), Maini and Horton (1966), Gifford (1967) and Steneker (1974) have looked at the influence of disturbance on regeneration of aspen particularly by suckering.

The aspen canopy may severely suppress growth of other tree species in lower strata (Lees 1966; Steneker 1967). Aspen itself is very shade intolerant and regenerates poorly under dense canopy or understory (Gates 1930; Maini 1972).

The ecology of aspen and associated vegetation in relation to succession after fire in Alaska is extensively treated by Lutz (1956). In the Rocky Mountains the same subject was discussed by Clements (1910), Pearson (1914), Sampson (1916) and Baker (1918). Some attention was paid to the understory in these treatises but it was not until 1925 that Baker made a detailed analysis of aspen forests in the central Rocky Mountains. This work included descriptions of aspen site requirements, diseases, associated flora and fauna and reproduction. Subsequent work in western Canada by Bird (1932) described aspen groveland of the prairie provinces. Moss (1955) described the poplar association in Alberta.

Until recently aspen studies of an intensive nature have been restricted to the United States, for example Gates (1930) for northern lower Michigan, Kittredge (1938) for Minnesota and Wisconsin. The

ecology of aspen in western regions of North America has been studied by Cottam (1954) in Utah, Lynch (1955) in Montana, Crowther and Harper (1965) in Utah, Morgan (1965) in Colorado, Oswald (1966) in Wyoming and Reed (1971) in Wyoming.

One of the most striking vegetational features of the western Canadian Rocky Mountain National Parks, especially Jasper and Banff district, is the sharp boundary which separates many stands of aspen from surrounding coniferous forest (Fig. 1). At any season the separation of aspen from lodgepole pine or white spruce is distinct especially when viewed from a high vantage point. During the winter period, when leafless deciduous trees stand out in a dark green background of conifers; or when leaf colouration associated with fall creates the perfect situation to distinguish the aspen from surrounding vegetation, it is obvious that some unique conditions are contributing to the creation of a niche suitable for aspen and, at this time, repressing the growth of other tree species.

Avalanche activity is common throughout the Rocky Mountains. Large fan-shaped scree slopes and avalanche paths occur frequently in the steeper sided valleys. Aspen is often found to be growing over the avalanche fans (Fig. 2), but only in the disturbed material. The edge of the fan frequently coincides with the transition from aspen to coniferous or other vegetation type. It is possible that the disturbance of soil associated with new materials introduced from uphill strata is important to the continued survival of aspen on these sites. Furthermore, the avalanche sites are frequently in broad shallow

FIGURE 1

Aspen stand No. 4 during summer months, Patricia Lake, Jasper. Pyramid mountain behind. Showing the sharp boundary between an aspen stand and adjacent conifer *(P. contorta)* forest.

FIGURE 2

Aspen stand No. 5 below Roche Bonhomme, Jasper on Maligne Lake road. Showing aspen stand in typical situation on avalanche fan below gully.

depressions in the mountain slopes. Groundwater and annual runoff are often concentrated in these depressions which may provide favourable conditions for aspen growth. Some aspen stands are not situated on steep avalanche-prone slopes but spread over wide alluvial fans in the bottoms of U-shaped river valleys. The particular soil types and physical fractions within the soil profile may be partly responsible for the persistence of aspen in these locations.

Although not a recent phenomenon, fire has had an influence in the past on the distribution of vegetation cover within the parks. While resinous, coniferous forest is more prone to intense hot fires, but can in certain cases be stimulated to regenerate by seed from fire-opened cones (e. g. *Pinus contorta*), deciduous forest cover may burn less intensely. Aspen is particularly well adapted to regenerate after light fires, which may have had an influence on the present distribution of this tree in the parks. Fire may also prove to be an important measure in maintaining aspen as part of the forest cover in the parks. In particularly severe winter conditions, or when over population occurs, elk have been partly responsible for the destruction of mature aspen (Krebill 1972). When regeneration occurs by suckering, elk may also be responsible for browsing the suckers repressing or preventing growth of second generation aspen. The influence of physical and biological factors upon the distribution of aspen in the parks is complex, but may be partly resolved through the detailed interpretation of plant distribution, soils, climate and moisture regimes within and between stands.

Objectives of Study

1. To describe and compare the floristic, structural and physical features of aspen dominated forest stands throughout Jasper and Banff National Parks.
2. To classify the aspen stands described, on the basis of the features studied.
3. To evaluate over a twelve month period, the monthly water regime in soils under three aspen stands chosen as representative of all stands studied.
4. To provide information on the successional status of all aspen stands studied, and the nature of these stands relative to others described from throughout northwest America.

SYSTEMATICS AND AUTECOLOGY OF ASPEN

Systematics

Trembling or quaking aspen (*Populus tremuloides* Michx.) belongs to the group Amentiferae and is a member of the family Salicaceae.

The family is represented in North America by only two genera, the entomophilous genus *Salix* and the anemophilous genus *Populus*.

The genus *Populus* is divided into five sections representing species from North America, Europe, Asia and Africa. *Populus tremuloides* and *P. grandidentata* are the only two North American species within the section Leuce. The closest species to *Populus tremuloides* is *P. tremula* widely distributed in Eurasia.

In Alberta, Moss (1959) lists six species:

Populus acuminata Rydberg

Populus angustifolia James

Populus balsamifera Linnaeus

Populus sargentii Dode

Populus tremuloides Michaux

Populus trichocarpa Torrey and Gray

The Alberta species have ranges that overlap in the southwest of the province and it is here that most of the hybridization occurs, both within and between sections (Brayshaw 1960).

Populus tremuloides is recognized as having four varieties distributed across Canada. The western variety *Populus tremuloides var. aurea* (Tid.) Dan. is distinguished by its deep golden colouration

during leaf fall, shorter calyces and larger anthers than those of the other three *P. tremuloides* varieties (Sudworth 1934; Brayshaw 1960).

Distribution in North America

Populus tremuloides is the most widespread deciduous tree in North America (Harlow and Harrar 1941) being distributed over 110° longitude and 47° latitude (USDA 1965) (Fig. 3). In an east-west direction aspen ranges from the coast of Labrador and Newfoundland west to Yukon and Alaska. From the northern tree line of the boreal forest it extends south to northern Mexico at progressively higher elevations in the Rocky Mountains (Graham *et al.* 1963). Aspen extends into the eastern deciduous forest as far as southern Ohio.

Optimum development of aspen occurs in western Colorado and Utah (Morgan 1969) and is coincident with aspen growth over large areas. Aspen is found at its northern limits up to 1,740 m (5,800 ft.) above sea level (ASL) (Sudworth 1934). Proceeding south there is an increase in elevation at which the species will grow such that in northern Mexico it is found at 3,200 m (10,000 ft.) or more ASL. Unlike many woody species aspen runs the gamut of zones from the montane to the alpine (Daubenmire 1943).

Life History

Aspen is normally dioecious although a few trees are monoecious (Strothmann and Zasada 1957; Mennel 1957; Maini and Cayford 1968).

FIGURE 3

Natural distribution of *P. tremuloides* in North America.


P. Tremuloides
P. Tremuloides Var Aurea

Baker (1918) reported that aspen in the western United States produced little seed due to the low number of pistillate trees, the low viability of aspen pollen and great distances separating flowering trees of the opposite sex. Seed crops of large volume are produced every five years in the Eastern United States, according to the USDA (1965). When seed is produced germination will take place immediately under moist conditions (Moss 1938). Within a few weeks of dispersal, seed viability decreases substantially and can only be maintained at high levels under controlled temperature and humidity conditions (Faust 1936).

The alternatives of reproduction by seeding or adventitious shoots, of which the latter appears to be the most frequently encountered mode, are determined by the suitability of conditions prevailing in any one region. Suckering gives rise to genetically identical clones (Cottam 1954; Maini 1960; De Byle 1962).

Suckering is controlled by numerous factors amongst which are age and vigour of the parent tree (Rowe 1956), root thickness and depth from the soil surface (Maini 1960), soil temperature (Maini and Horton 1966), soil aeration (Maini and Cayford 1968), competition by shading from surrounding vegetation (Maini and Horton 1966), any disturbances which increase soil surface temperature (Horton and Hopkins 1965), and apical dominance (Steneker 1974).

Growth of sucker sprouts and seedlings is rapid in the first seven to ten years. In the case of suckers, site conditions do not affect the growth rate substantially but seedlings in poorer sites will not grow well after the initial twelve months. After twenty years,

growth of aspen is slowed (Clements 1910) and senescence begins around eighty years (Zehngraff 1947). Graham *et al.* (1963) report aspen growing to one hundred fifty years although after this time decay in the heartwood can be well advanced (Baker 1925). On poor sites trees may become decadent as early as forty years.

Since aspen is predominantly clonal in the Rocky Mountains, one clone may reach considerable age although the extant trees are only sixty to seventy years old.

In Alberta, Moss (1938) reported heavy seed production of aspen in the Edmonton region every three to seven years. Very rarely do the seeds manage to germinate and become established. The age of aspen in Alberta seldom exceeds one hundred twenty years, the most significant factor curtailing the longevity of the trees being heartrot fungus *Fomes ignarius* L., *Radulum cascarion* (Morg.) Lloyd and *Corticium polygonium* Pers. (Davidson and Prentice 1967).

THE STUDY AREA

Geology and Geomorphology

The mountain ranges of Jasper and Banff all trend in a northwest-southeast direction. Four major thrust faults trending in the same direction as the mountain ranges expose Precambrian sandstones, slates and occasionally carbonates, Paleozoic limestones and Mesozoic sandstones with shale. The Devonian limestones are the most important element in the Paleozoic succession of the eastern ranges forming all major peaks there (Allen, Warren and Rutherford 1932).

From Jasper southeast to Banff the lower cliffs of many mountains are formed of Cambrian quartzites overlain by thick limestone strata of Jurassic age (North and Henderson 1954). The main peaks overlying the valley cliffs are predominantly sedimentary limestones and shales with some sandstones.

Glaciation during the Pleistocene period covered the Rocky Mountains in the two parks with ice to an elevation of 2,400 m (8,000 ft.) ASL. By the end of the period the ice had produced broad valley floors and steep-sided valley walls. Deposition of glacial till during glacial retreat accompanied by variable depths of wind and water borne deposits in the valley bottoms resulted in the present day surficial geology of the parks (Heusser 1956).

Post-glacial weathering and erosion have created extensive talus slopes and avalanche fans in numerous localities, bringing rock fragments of strata from upper elevations into contact with glacial till, river

deposited sands and silt, or bare bedrock.

The North Saskatchewan river flows south and then east from the Sunwapta divide through the north end of Banff National Park. The Bow river originates at the Bow glacier and flows south and then east through the south of the Park. The main valley running in a northwest-southeast direction in Jasper carries the Sunwapta river from the Columbia icefields to join with the Athabasca river northeast of the icefields.

Soils

The soils in the National Parks have been studied only in a few localities to date and detailed soil maps are not available. Glacial till is the parent material of the majority of the soils in the montane zone, but extensive wind blown and water deposited materials have created varied soil profiles especially in the valley bottom areas.

Soil surveys completed within the Park boundaries to date reveal a very complex system in which soil types change frequently over very short distances. Generally it can be stated that Eutric Brunisols and Luvisols predominate with Regosols on the steeper slopes or at higher elevations.

Climate

The northern Rocky Mountains create a topographic obstacle to polar maritime air masses which move inland from the north Pacific

during the period September to June. The maritime air is progressively cooled as it is forced up by the mountains and on arrival over the parks resembles inland continental air (Heusser 1956). During the summer Pacific air from the west mixes with continental air and is indistinguishable from it on arrival over the continental divide. The general effect of these air movements is to create maximum turbulence and precipitation during June and July. Temperature maxima occur in July and August (Figs. 4 and 5).

The winter situation is similar inasmuch as air from the north and west rises over the mountains to be cooled and contributes maximum precipitation in February and March, and minimum temperatures January to February.

Logging and Fire

Lumber extraction, silver, graphite and coal mining, stimulated by the building of the railroads and later the highways, preceded or followed the establishment of the Rocky Mountain National Parks. Large tracts of forest were burned either accidentally or by design during the pioneer operations, creating situations well suited to the establishment of aspen. However, in the past sixty years a rigorous fire control policy has been maintained by Parks Canada. The predominance of lodgepole pine (*Pinus contorta* Doug. var *latifolia* Engeln.) over most of the lower mountain slopes indicates that this species has succeeded probably owing a great deal to past fires.

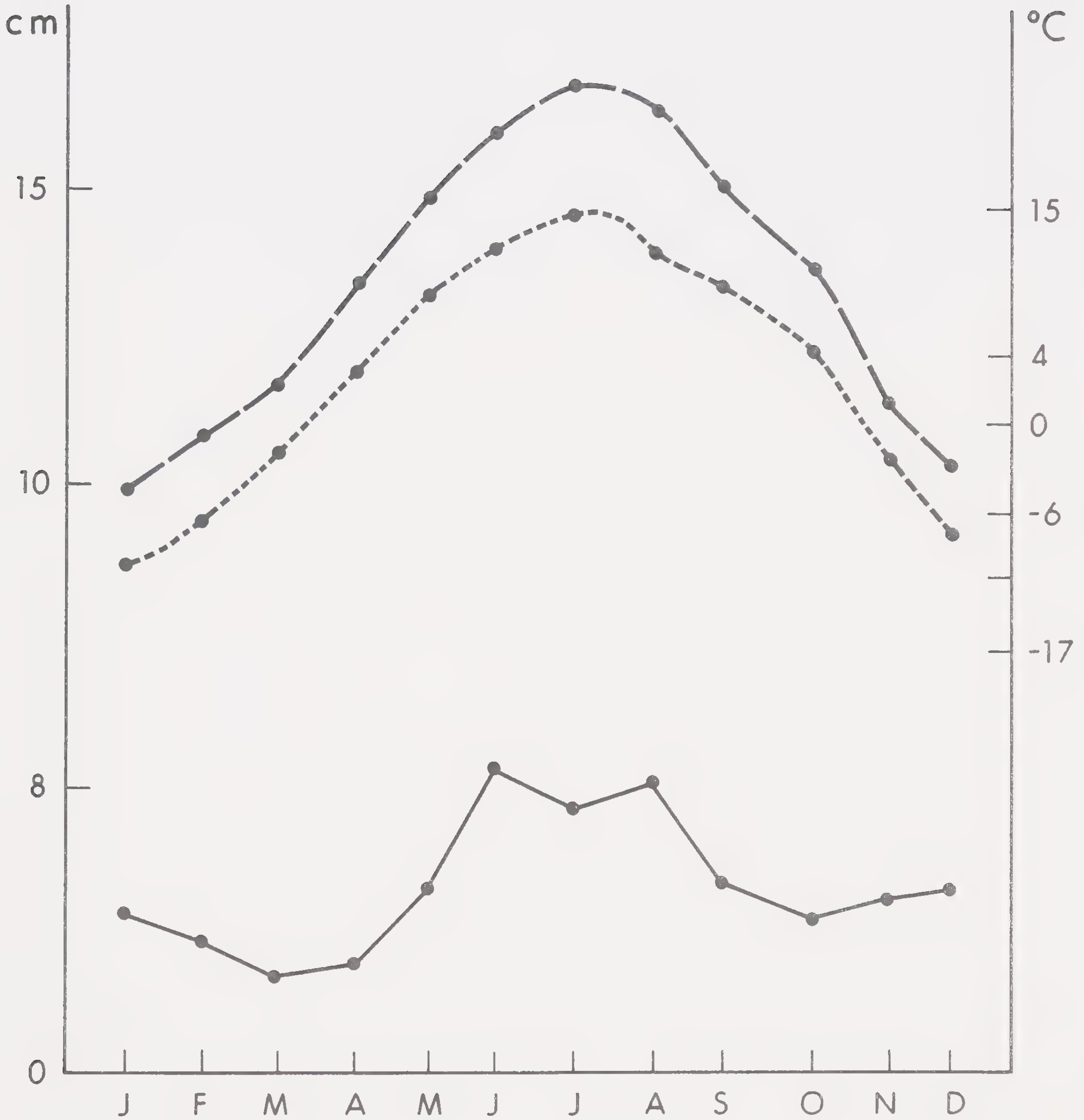
FIGURE 4

Climatological data for Jasper townsite, Jasper National Park, developed from thirty year records (Canada Department of Transport).

Mean monthly total precipitation

Mean daily maximum temperature

Mean daily temperature



cm
°C
15
10
8
0
15
4
0
-6
-17
J
F
M
A
M
J
J
A
S
O
N
D

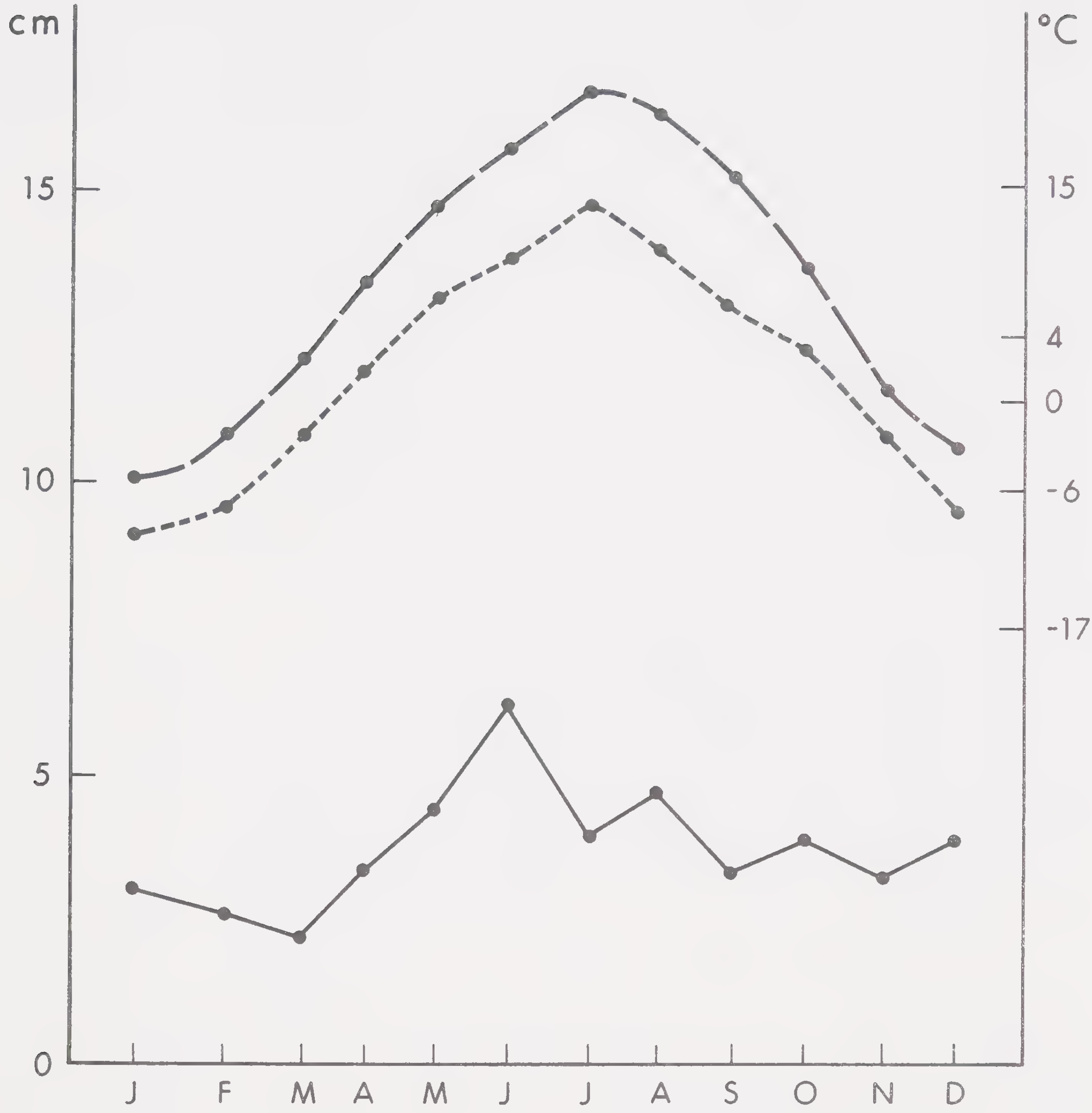
FIGURE 5

Climatological data for Banff townsite, Banff National Park, developed from thirty year records (Canada Department of Transport).

Mean monthly total precipitation

Mean daily maximum temperature

Mean daily temperature


cm
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METHODS

Criteria of Stand Choice

The aspen stands studied were all located in the montane zone of the Parks, *sensu* Rowe (1972). The montane zone in Jasper extends from the Athabasca river at 990 m to 1,560 m, and is marginally greater in elevational extent but at an overall lower elevation than the same zone in Banff which extends from the Bow river at 1,380 m to 1,770 m (Stringer and La Roi 1970).

Field reconnaissance aided with aerial photos was used to locate as many areas as possible of aspen-dominated vegetation throughout the parks. The areas so located were plotted onto 1:190,000 scale maps. Although many small groups of aspen occur throughout the parks, many in inaccessible or remote areas, as broad as possible a representation of stands was sought. To provide conditions under which sampling would be least affected by 'edge' effects, when the size of a stand equalled or exceeded ten hectares, closer inspection was made. Whenever possible, canopy composition of at least 50 per cent aspen was sought, as this was thought to represent aspen stands found throughout the parks. Any recent human disturbances, including road rights of way, ditching or trail building were avoided. However, reasonable accessibility on foot from a vehicle right of way was considered important. If, after size and vegetational composition criteria were satisfied, and no other constraints were evident, the stand was considered appropriate for study.

The study areas were confined within the boundaries of Jasper and Banff National Parks (Figs. 6 and 7). Eight stands in Banff and four in the north of Jasper are situated in the Front ranges of the Rocky Mountains while the remainder of the stands are in the Main ranges. All but five stands (5, 6, 12, 15, 20) are located in Jasper's Athabasca Valley or Banff's Bow Valley.

Vegetation Analysis

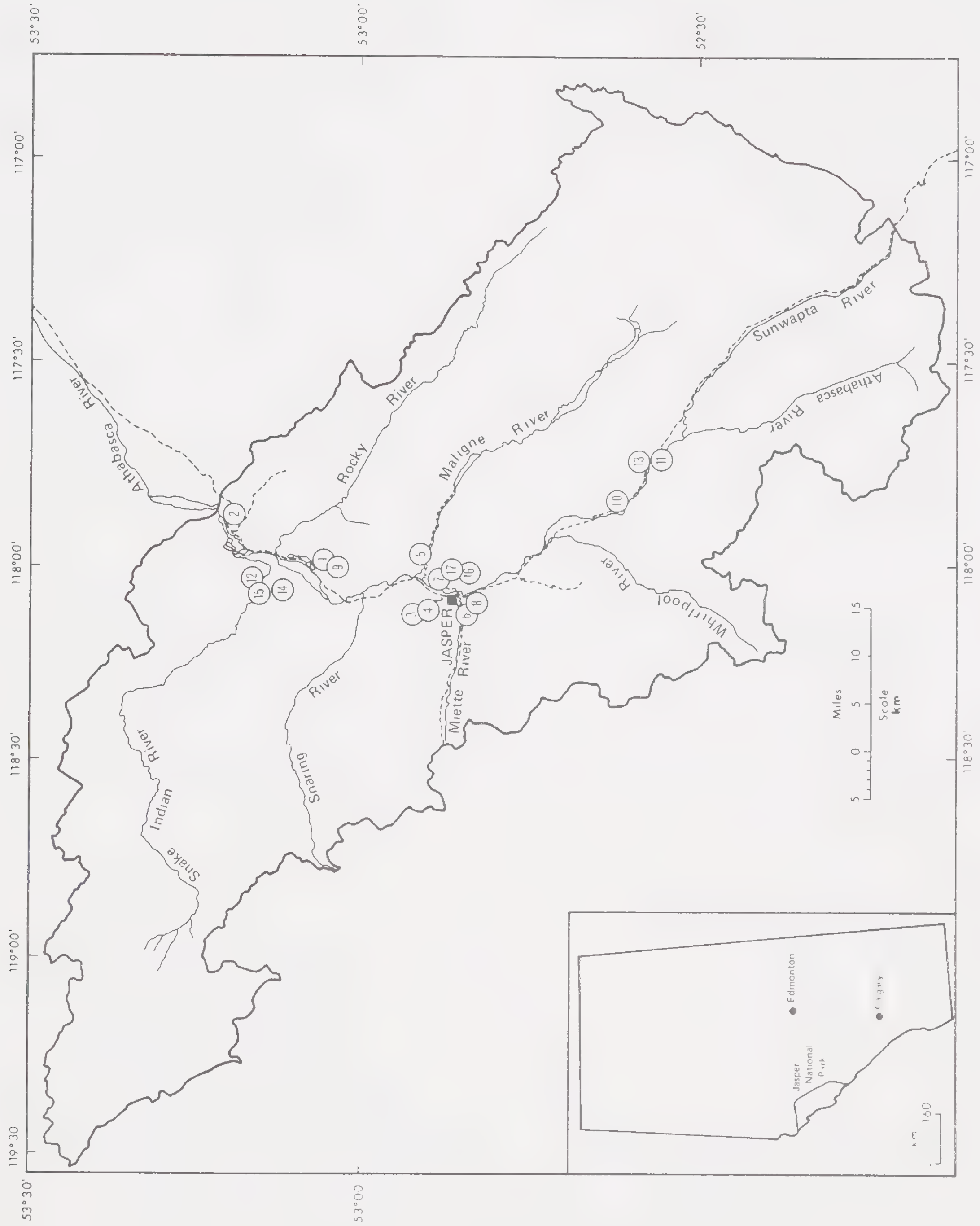
Intensive investigations were made of the floristic composition of each stand over a period of two summer seasons. At the same time, soil sampling was carried out to quantify the chemical and physical attributes of soil supporting each stand.

Throughout a period of twelve consecutive months, October 1971-1972, soil moisture by volume was assessed for three selected stands using neutron probe techniques. The month to month and season to season changes of soil moisture were considered in the context of aspen community type and vegetation characteristics as well as distribution features of aspen forest throughout the parks.

The sampling units consisted of nested quadrats. Quadrat frames were constructed of nylon rope pinned down at each corner. Quadrats 10 m X 10 m were used for trees ($>$5 cm dbh), 2 m X 2 m for shrubs ($<$5 cm dbh $>$30 cm tall) and 1 m X 1 m for herbs and dwarf shrubs (all non-woody plants), bryophytes and lichens. Any bryophytes or lichens on the bole of trees or fallen logs were sampled within the 1 m^2 quadrats. A seven point cover scale was used to estimate cover classes:

FIGURE 6

Location of stands in Jasper National Park. Location of Jasper National Park in Alberta (inset). (For example 7 -- Aspen stand.)



53°30'
53°00'
52°30'
117°00'
117°30'
118°00'
118°30'
119°00'
119°30'
Athabasca River
Rocky River
Maligne River
Sunwapta River
Athabasca River
Whirlpool River
Miette River
JASPER
Snaring River
Snake Indian River
Miles
Scale
km
0
5
10
15
Edmonton
Jasper National Park

FIGURE 7

Location of stands in Banff National Park. Location of Banff National Park in Alberta (inset).

117°00'
116°30'
116°00'
115°30'
52°00'
51°30'
51°00'
North Saskatchewan River
Clearwater River
Red Deer River
Bow River
Spray River
BANFF
25
24
20
23
21
22
18
19
Miles
5 0 5 10 15
Scale
km
Edmonton
Banff National Park
Calgary
km
0 160

+ (1%) 1 (1-5%) 2 (5-15%) 3 (15-25%) 4 (25-50%) 5 (50-75%) 6 (75-100%). Cover class midpoints were used in generating means and prominence values (see below).

Specimens unidentified in the field were collected for later identification. Voucher specimens are deposited in the University of Alberta herbarium, (ALTA). Nomenclature of vascular species is according to Moss (1959) and of non-vascular species according to Bird (1968) and Lawton (1971).

Tree basal area was estimated from the centre of each tree quadrat using a 10X basal area prism.

Tree density was computed from the total number of trees in each quadrat expressed as numbers of stems per hectare.

Tree stratum height was determined using a Spiegel Relaskop taking readings from dominant trees throughout the stand. Dominance was judged from the height of each tree relative to the entire canopy.

Tree canopy cover was photographed from the centre of each 10 m^2 quadrat using a camera projected vertically. Canopy cover was computed from negatives according to the methods of Beil (1966).

Stand age determinations were based upon cores taken at diameter breast height from each tree nearest the centre point of each 10 m^2 quadrat.

A 200 m base line was positioned centrally down the long axis of the stand and divided into twenty 10 m intervals. Twenty random numbers up to a maximum value of ten dictated the position of lateral lines drawn from the base line within each 10 m interval. The position

of quadrats was determined from a second series of random numbers pairs. Each pair could have a minimum value of zero thereby placing the quadrat on the axial line up to a maximum value of 99 m placing the quadrat this distance perpendicular to the axial line. Odd numbers were taken left of the axial line, even numbers to the right.

A small number of quadrats were analyzed to determine the total number required to obtain estimates $\leq$ 10 per cent standard error of the mean cover of dominant species in each stratum. The formula $n = t^2 \ S^2/S\bar{x}^2$ was used where n is the number of quadrats, t the significant difference at the 10 per cent level of confidence, $S\bar{x}^2$ the variance of the sample. The variance was estimated from $S\bar{x}^2 = W^2/_9$ where w is the range of cover class midpoint values obtained (Husch 1963). A sample consisting of twenty quadrats was found to give acceptable results within the limits stated.

Soils

Three soil pits were located at intervals of 0, 60 and 120 m along the base line. The positions of the pits to left or right of the line were determined using random numbers of the same manner as that employed for quadrats.

Three samples were taken at each of three depths (0-10 cm, 10-20 cm, 20-40 cm) in each pit, corresponding closely with the rooting depths of herbs, granes, shrubs and trees.

Combined samples from each depth in each pit were sieved, and all material passing the 2 m sieve was analyzed for nitrate nitrogen

(phenoldisulphonic acid method); potassium (ammonium acetate method); phosphorous (modified Bray method); per cent available soil water (1/3 bar per cent - 15 bar per cent, ceramic plate extraction); soil reaction and conductivity (1:2 soil:water paste, glass electrode) and texture (Bouyoucos 1951, modified by reciprocal shaking for one hour).

After floristic and pedological data were available, four of the twenty-five aspen stands were chosen for intensive investigation of seasonal soil moisture flux. The stand in Banff was not accessible on a regular basis for sampling and was abandoned in the winter of 1972. The three remaining stands in Jasper were considered broadly representative of the sampled aspen stands and soil types under these stands throughout the two parks.

The central area of each stand was divided into twenty-five one hectare units of which eight were chosen randomly for sampling.

Within each of the eight random hectares, aluminum tubing 3.25 cm inside diameter and 1.5 m long was placed in a hole approximately 1.4 m deep driven into the ground with 5 cm gas piping. Each tube protruded about 30 cm above ground although in particularly rocky ground it was impossible to drive a hole deeper than 75 to 90 cm.

A Nuclear Chicago soil neutron probe (model P19) was used by permission of the Soil Science Department, University of Alberta. During the third week of each month October 1971 to September 1972 inclusive, readings were taken in the three Jasper stands (2, 5, and 13).

The probe was first checked for standard count rates in the shield. In the event that the standard count varied more than ±3 per cent about a given mean, the probe was checked for battery or lead defects. The probe was then lowered down the aluminum tube 30 cm below the soil surface. This gave a reading of the soil moisture in the top 50 cm of soil since neutron dispersion is in approximately a 20 cm spherical mode from the source. After five consecutive readings at one depth the probe was lowered 15 cm where another five readings were taken. This procedure was continued to the bottom of the access tube, and repeated for all eight access tubes in each stand.

Readings in counts per minute (cpm) were plotted on a standard calibration curve supplied with the probe derived from a loam soil of 33 per cent each sand, silt, and clay. The readings from the curve determined soil water content as percentage by volume.

Ordination and Cluster Analysis

Species importance within each stand was calculated as a prominence value (PV) from the formula $PV = C \times \sqrt{F}$ where C is cover percentage and F quadrat frequency as percentage (Stringer and La Roi 1970). This is a modification of the procedure used by Beals (1960).

Coefficients of similarity for each stand were calculated using the formula $C = (2W/a+b)100$ (Kulczinski 1937), where C is the coefficient of similarity, W the sum of the lowest PV's of all species common to both stands, and a and b total PV's of all species in stands A and B respectively. Coefficients of dissimilarity (100-C) were used in the

construction of two dimensional ordinations following the method of Bray and Curtis (1957), using the Department of Computing Science, University of Alberta programme.

For vegetation data organized in a continuous pattern, ordination techniques are most appropriate. In situations of discontinuous, non-aggregated sets of data, cluster analysis techniques are most appropriate to assemble the isolated items (stands in this case) into aggregate units.

The prominence values previously computed were employed in the Pritchard and Anderson (1971) cluster analysis, from which nearest neighbour, furthest neighbour, group average, centroid and minimum variance clusters were generated and displayed in dendrogram form. The Department of Computing Science, University of Alberta, supplied the programme.

RESULTS AND DISCUSSION

Vegetation

The 'stand' in this context refers to a single geographic entity defined by aspen dominance in the tree stratum. Aspen 'community types' are, abstract assemblages of stands, and are described on the basis of understory species. Thus community types are points (noda Poore 1962) along a vegetation gradient which may be due to a complex of environmental and time factors. No attempt was made to quantify the time-dependent variables e. g. fire, anthropogenic and animal disturbance, which may have been partly responsible for creating the community types as they exist at present.

Classification

Field observations and data provided some initial indications of the aspen stands as they were related to community types. Cover values for all species were converted to prominence values, since it was considered that cover alone would not discriminate sufficiently for separation of stands that are only marginally different.

The accuracy with which the ordinations portrayed stand dissimilarities was tested by correlation coefficients between each interstand distance as plotted and the dissimilarity value for all stand pairs. The correlation coefficient suggests that the ordination is an accurate representation of interstand relationships.

Although the X, Y axes ordinations proved to be helpful in

separating similar and dissimilar stands, cluster analysis was required to clarify the interrelationships of some units. The five cluster analysis dendrograms were broadly similar in subdividing the stands, although the least discrimination was shown in nearest neighbour clustering. The minimum variance dendrogram is utilized (Fig. 8) since it most clearly demonstrates three clusters, evident in both ordination and the remaining dendrograms.

Ordination of all twenty-five stands utilizing both vascular and non-vascular species generated a plot (Fig. 9) in which most stands were aggregated in the central region and peripheral stands (1, 17, 18, 20, 21, 24 and 25) were poorly related to the 'core'. These same satellite stands were then removed from the matrix and ordination carried out on the 'core' (Fig. 10). A clearer separation of stands, and one which fitted well with the cluster analysis was achieved.

A small group of stands, 1, 19 and 23 were consistently identified together in all cluster dendrograms, but were more clearly separated by the ordination of core stands. All three stands have high PV's for *Elymus innovatus* (Table I). Both 19 and 23 have high recorded densities of *Picea glauca*.

In the twenty-five stand ordination, stands 21 and 22 were in the upper area of the central group (Fig. 9). The core ordination separated 22 from all others, and cluster analysis confirmed that both stands 21 and 22 were similar. The relatively low PV for *Elymus innovatus* in these stands is possibly affecting their relationship to all other stands. Since 21 and 22 are shown by ordination and cluster analysis

FIGURE 8

Cluster analysis dendrogram, using minimum variance clustering (Pritchard and Anderson 1971).

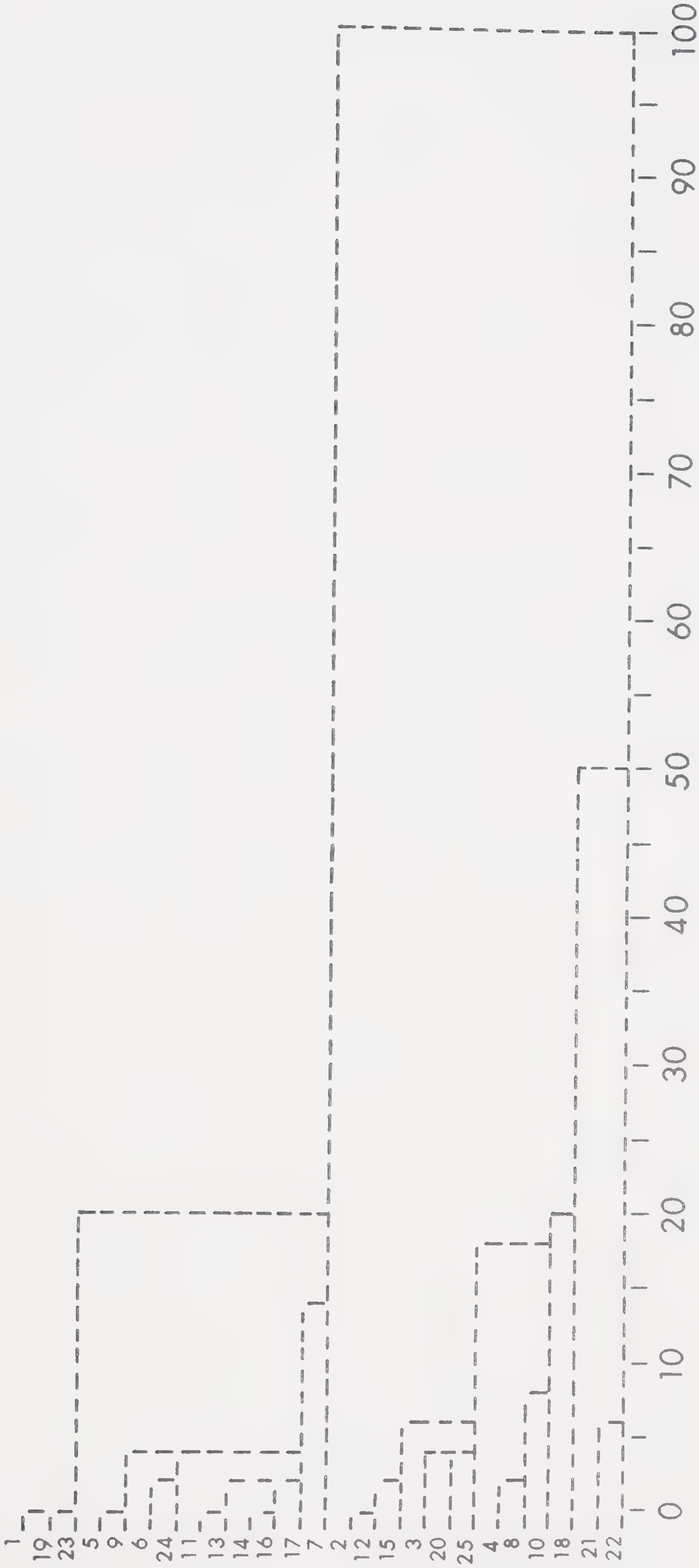

1
19
23
5
9
6
24
11
13
14
16
17
7
2
12
15
3
20
25
4
8
10
18
21
22
0
10
20
30
40
50
60
70
80
90
100

FIGURE 9

Community types on ordination field of twenty-five aspen stands.

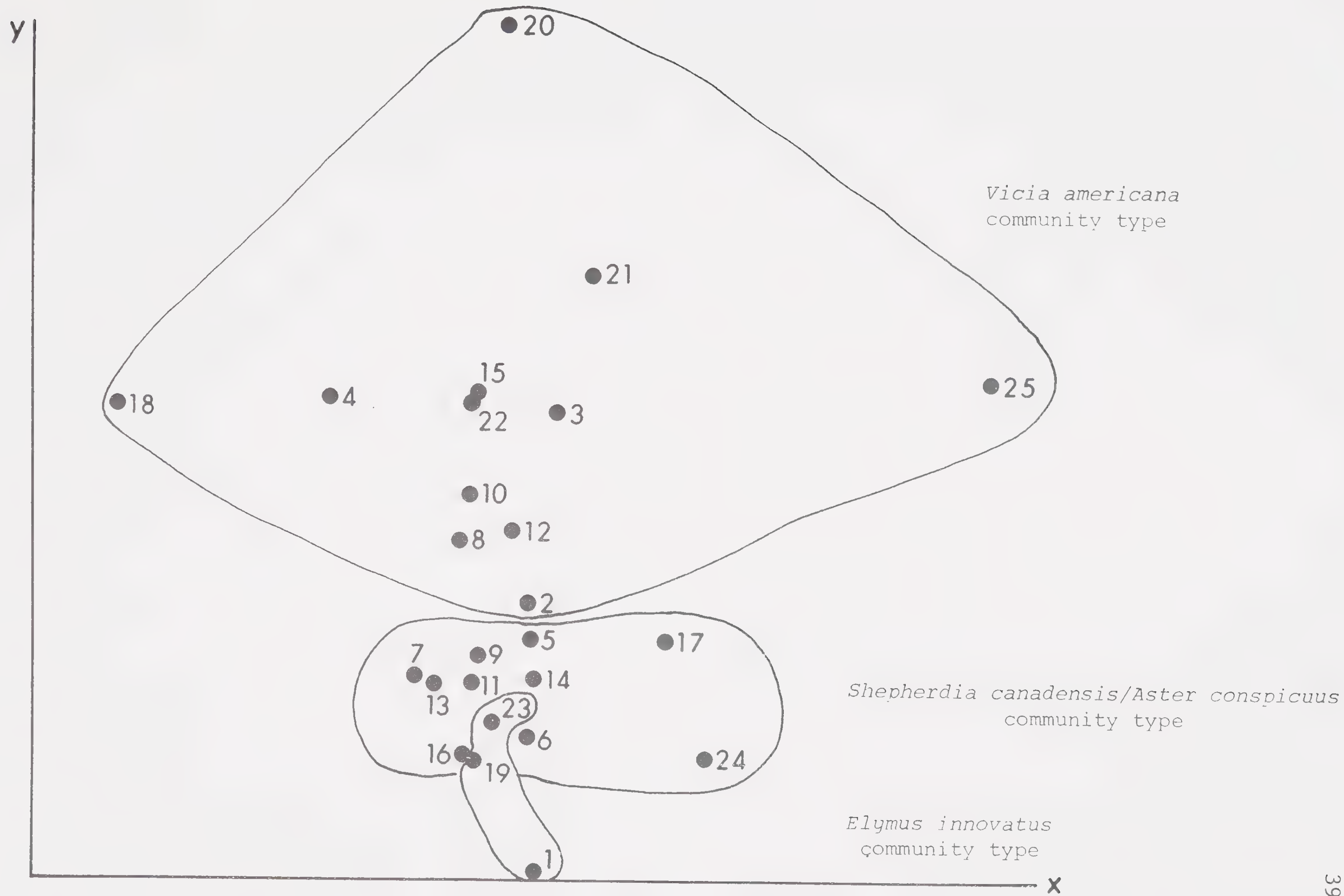

y
x
20
21
15
18
4
22
3
25
10
8
12
2
5
17
7
9
11
14
13
23
6
16
19
24
1
Vicia americana community type
Shepherdia canadensis/Aster conspicuus community type
Elymus innovatus community type

FIGURE 10

Community types as described on twenty-five stand ordination on ordination field of 18 aspen stands selected from twenty-five stands studied.

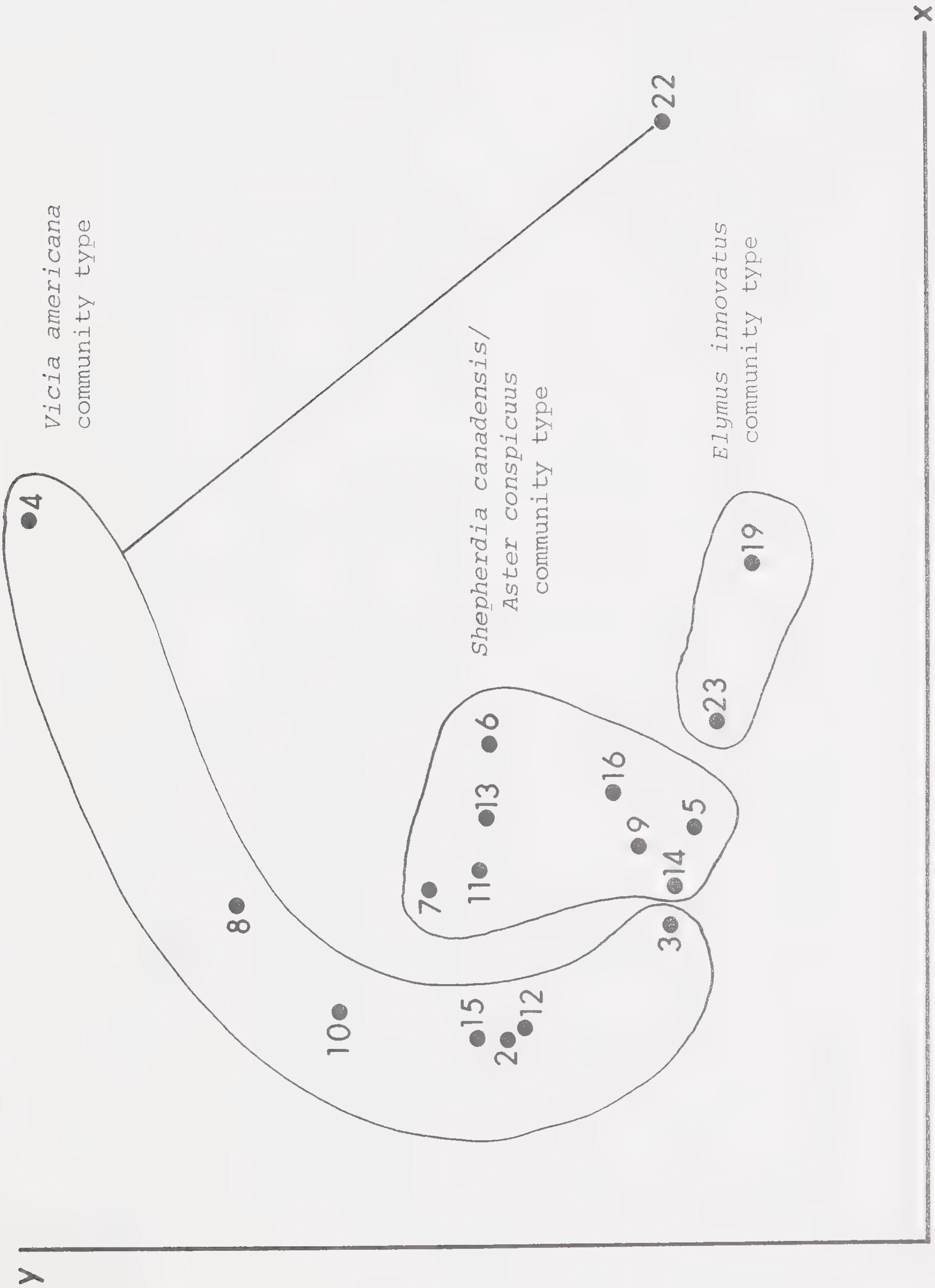

Vicia americana
community type
Shepherdia canadensis/
Aster conspicuus
community type
Elymus innovatus
community type
4
22
19
23
6
13
16
5
9
14
11
7
8
3
10
15
2
12
x
y

TABLE I

MEAN STEM DENSITY PER HECTARE OF TREE SPECIES AND PROMINENCE VALUES OF ALL VASCULAR AND NON-VASCULAR UNDERSTORY SPECIES BY COMMUNITY TYPE AND STAND

Species	COMMUNITY TYPE AND STAND																								
	Elymus innovatus			Shepherdia/Aster conspicuus										Vicia americana											
	19	1	23	9	24	16	13	7	14	11	6	5	17	21	15	4	22	10	20	18	25	8	12	3	2
TREES																									
Populus tremuloides (live)	83	45	59	93	64	120	94	153	142	181	140	85	95	123	112	221	85	66	180	75	70	115	106	84	55
Populus tremuloides (dead)	6	-	14	8	16	33	85	21	45	58	22	9	14	52	39	48	13	14	15	18	4	37	36	13	11
Populus balsamifera (live)	4	22	32	-	8	3	-	-	43	-	-	35	-	34	-	-	-	-	3	-	-	-	-	2	29
Populus balsamifera (dead)	-	3	6	-	-	-	-	-	10	-	-	11	-	2	-	-	-	4	-	-	-	-	-	-	-
Picea glauca	-	15	14	-	-	-	13	-	-	-	-	-	-	6	-	-	-	-	3	8	-	2	-	1	7
Pinus contorta	-	-	-	-	-	1	3	-	-	8	-	-	-	-	-	-	-	-	-	1	-	8	-	-	-
SHRUBS																									
Rosa acicularis	31	33	21	6	31	45	6	39	2	11	11	12	55	41	16	22	10	18	20	1	10	22	39	49	21
Shepherdia canadensis		3		1		11	38	84	84	27	80	T				38		64		T		65			13
Symphoricarpos albus	4					2			T			T	20	1	1		T		T	1			12		
Spiraea lucida			T	T		4			2		2		T				1		T	18	1	T	22		
Lonicera involucrata		1			T	T		1	T				15											2	3
Juniperus communis			1				1											35	1	4			T		
Juniperus horizontalis							T	T																	
Amelanchier alnifolia																									3
Viburnum edule		1							1		2	6									20	T		T	
Ribes hudsonianum		4																							4
Potentilla fruticosa			T																						
Cornus stolonifera		2																							3
Ribes lacustre			1																						
Ribes oxyacanthoides										T													T		1
Rubus strigosus											T		40												
Lonicera dioica												1	T												

TABLE I (Continued)

Species	COMMUNITY TYPE AND STAND																								
	Elymus innovatus			Shepherdia/Aster conspicuus										Vicia americana											
	19	1	23	9	24	16	13	7	14	11	6	5	17	21	15	4	22	10	20	18	25	8	12	3	2
DWARF SHRUB																									
Arctostaphylos uva-ursi	6		9	22	T	25	18	61		18					17	119	T	1		289		32	1		
Linnaea borealis		4				2	31	1		40	86							93	12	8		227		3	19
Rubus pubescens		T																						13	18
Vaccinium caespitosum																		T							
HERBS																									
Vicia americana	5		7	6		2			1		T		4	21	27	T	45	28	14	7			4	T	T
Aster conspicuus	2	1	9	13	65	4	2	4	3	4		3	68	22	8	T	12		12	T	95	T	5		T
Galium boreale	21	1	4	11		T	1	3				2	3	6		2	5		7	7			4	3	1
Castilleja miniata		T	3	8	1				T	1							2	T		T	T	9	2		T
Fragaria virginiana	17	T	19	T	4	3	24	T	T	13	T	T	2	78	T	T	6	179		21	4	10	1	11	3
Lathyrus ochroleucus	26	T	21	29		11	10	T	26	3	32	66	17	42	79	28	24	12	53	6		2	4	8	5
Aster ciliolatus	4	T	33	24	3	T	T	13		3	T	7	9		8	T	1	24	2			2	11	15	3
Achillea millefolium	T	T	4	10			T						T	5	2	T	7	T	1	1		T	2		T
Pyrola secunda	2	T		T	T		1	T	T	1	2	T	1			T		6	T			2			T
Vicia americana	5		7	6		2			1		T		4	21	27	T	45	28	14	7			4	T	T
Hedysarum boreale	21	1	7	1				1								T		T	2				1		T
Arnica cordifolia							T				15					24		T	T			2		T	
Smilacina stellata	3	T	T						T			4	6							3	T		T		T
Aquilegia brevistyla	T		1		10				3					31		T			2		77				
Epilobium angustifolium		T			14		1			T	T	16	T	19	T	T		1			66				
Viola rugulosa	T	T	3					T	37			6	5	1			1		11	T	7			1	74
Oxytropis campestris	T																		T	18					
Senecio lugens	8		1																9						
Erigeron glabellus						T	T							T						1			1	T	
Agoseris glauca			T					T									T			T					
Astragalus decumbens																	1			2					

TABLE I (Continued)

Species	COMMUNITY TYPE AND STAND																								
	Elymus innovatus			Shepherdia/Aster conspicuus										Vicia americana											
	19	1	23	9	24	16	13	7	14	11	6	5	17	21	15	4	22	10	20	18	25	8	12	3	2
HERBS (Continued)																									
Solidago lepida	T																								
Solidago multiradiata																				T					
Hedysarum sulphurescens																						T			
Zygadenus elegaus	T			3				T												4					
Anemone multifida	T		T	T				T							T		T		T	T			T		
Aster sibiricus															T					3			2		
Oxytropis deflexa						T														1					
Antennaria rosea				T																T					
Draba aurea																						T	T		
Solidago decumbens																									
Arenaria lateriflora																				T					
Trifolium repens											4												T		
Campanula rotundifolia	T			T				T											T						
Rhinanthus crista-galli			T												T					T			1		
Gentianella amarella	T					T																			
Habenaria obtusata		1	3	1		15	1	5									T		T	T			T		
Senecio pauperculus	2						T									2			T	18			1		T
Astragulus striatus						2								2			1		1	7				T	
Taraxacum officinale	T		4			1					T		1												
Viola adunca	T		T	3		T		T			T		T	1		T	3	T	1				T		
Mitella nuda											T				2									T	
Astragulus alpinus																									1
Senecio pseudaureus																									2
Oxytropis splendens						1								T			T								
Potentilla gracilis			T																				T		
Oxytropis sericea		T	2																						
Smilacina trifolia																									T
																									T

TABLE I (Continued)

Species	COMMUNITY TYPE AND STAND																								
	Elymus innovatus			Shepherdia/Aster conspicuus										Vicia americana											
	19	1	23	9	24	16	13	7	14	11	6	5	17	21	15	4	22	10	20	18	25	8	12	3	2
HERBS (Continued)																									
Erigeron perigrinus																			T						1
Equisetum scirpoides																									T
Cornus canadensis							8			1	12											28		7	35
Petasites sagitata									T		T		12					T						2	3
Pyrola asarifolia		5					T				4	T				T					T	2		9	4
Clematis verticellaris		T	3	T	T								T			1			T		17				T
Disporum trachycarpum		T			7							4										T		2	
Lilium philadelphicum				T																					T
Mertensia paniculata									T		T	2	37	30				2						3	36
Equisetum pratense												7												21	1
Osmorhiza chilensis																								8	
Geum alepicum																								T	
Smilacina racemosa									T																T
Equisetum arvense																								6	
Equisetum palustre																									T
Cerastium vulgatum																								4	
Galium triflorum																								1	
Petasites palmatus																								18	27
Aralia nudicaulis												T	36												
Anemone canadensis																								43	
Equisetum sylvaticum																								1	
Viola renifolia		T																T						3	
Delphinium glaucum		7							T			4													
Stellaria longipes												3													
Heraclum lanatum																					3				

TABLE I (Continued)

Species	COMMUNITY TYPE AND STAND																								
	Elymus innovatus			Shepherdia/Aster conspicuus										Vicia americana											
	19	1	23	9	24	16	13	7	14	11	6	5	17	21	15	4	22	10	20	18	25	8	12	3	2
GRASSES AND SEDGES																									
Elymus innovatus	424	484	364	264	296	281	204	172	251	198	327	316	232	35	110			109	21	70	35	98	100	19	157
Festuca subulata																				28					
Carex eburnea	1	2					T								2					1			T		
Muhlenbergia sp.				T																				2	
Oryzopsis pungens				T																					
Poa interior	T					T																			
Bromus sp.																							8		
Poa pratense																							T		
Koeleria cristata																							T		
Calamogrostis canadensis																									
Agropyron dasystachyum																			97						
Calamogrostis rubescens															104				20						
Cinna latifolia																								T	
MOSSES																									
Brachythecium salebrosum	T	T	T	T	12	2	2	2	3	3	6	T	2			T		3	T	T		4	T	5	
Amblystegium serpens				T		T		T	T		1			3			T	T	T		3	1			
Pylaisiella polyantha		T	T						T																
Pleurozium schreberi											2													T	
Eurynchium pulchellum											T								T						
Campylium hispidulum											T														
Campylium stellatum											2														
Drepanocladus aduncus								T																	
Mnium sp.											T														
Drepanocladus uncinatus																						2			

TABLE I (Continued)

Species	COMMUNITY TYPE AND STAND																								
	Elymus innovatus			Shepherdia/Aster conspicuus										Vicia americana											
	19	1	23	9	24	16	13	7	14	11	6	5	17	21	15	4	22	10	20	18	25	8	12	3	2
MOSSES (Continued)																									
Grimmia sp.										T															
Bryum sp.											1														
Distichium inclinatum						T																			
Pohlia nutans						T					T					T									
Ditrichum flexicaule							T		T					T							T			T	
Distichium sp.																									T
Hypnum cupressiforme		T																							
Dicranum elongatum													T											T	
Plagiothecium striatellum																								T	
Rhytidiadelphus squarrosus												T	T												
Rhacomitrium heterostichum												T													
Distichium capillaceum		T																							
Mnium orthorhynchium									T																
Plagiothecium denticulatum					T							T													
Homallothecium aeneum									T																
Ceratodon purpureus									T																
LICHENS																									
Stereocaulon tomentosum																						T			
Cladonia multiformis											T														
Cladonia conista								T																	
Cladonia gracilis																T									
Cladonia cornuta								T																	
Cladonia pyxidata										T	T														
Cetraria pinastre											T														
Peltigera canina						T				T	1									T		7			
Peltigera horizontalis																								T	

to be similar to each other and closely related to the group 3, 4, 8, 10, 18, 20 and 25 they are included within this major group.

The group 3, 4, 8, 10, 18, 20, 25 includes stands 2, 12 and 15 in all clustering techniques except centroid and nearest neighbour. Both ordinations identify these stands in the 3, 4, 8, 10, 18, 20, 25 cluster, to which they are considered to belong. Relatively low PV's for *Elymus innovatus* in 2, 12 and 15 similar to other stands in the group, was helpful in resolving the problem.

A second major group of stands, consistently including 5, 6, 9, 11, 13, 14, 16, 17 and 24 occurs in all ordinations and cluster analyses. Stand 7 is included in this group in both ordinations, minimum variance and group average clustering, but is excluded in centroid, furthest neighbour and nearest neighbour clusters. In these latter, 7 is most closely affiliated with 8 and 10, possibly due to their mutual relative high PV's for *Shepherdia canadensis* and *Arctostaphylos uva-ursi*. Dissimilarity values were of no assistance in placing this stand inside or outside the major group. It was decided that, based upon the prominence of *Elymus innovatus* relative to stands of the 2, 3, 4, 8, 10, 12, 15, 18, 20, 21, 22, 25 cluster, 7 was included with the 5, 6, 9, 11, 13, 14, 16, 17, 24 group. It is evident from the ordination, that *Elymus innovatus* as a major species influences the relationship of the stands along the Y axis. It is possible that stands 1, 19 and 23 previously separated are a sub-group of the major cluster 5, 6, 9, 11, 13, 14, 16, 17, 24 and 7. For the purposes of this study, 1, 19 and 23 are considered independent but closely related to the major cluster.

As described on the ordination field (Fig. 9) three community types are recognized. Minimum variance and group average clusters showed the closest fit with the ordination.

Elymus innovatus Community Type

The three stands dominated in the understory by *Elymus innovatus* occurred at somewhat higher elevations (1,380 m - 1,650 m) in Jasper and Banff (Table II). Canopy cover is lower than in the other community types. Stem density of aspen is also low relative to other stands surveyed. *Picea glauca* occurs in two out of the three stands, and contributed 13 per cent of the total mean density of all live trees. *Populus balsamifera* indicative of moist to wet soil conditions is also an important element in this community, accounting for 19 per cent of the total mean density. The mean age of these stands was greater than that of stands in the other community types.

The mean total species richness of this community type is greater than those of either of the other community types (Table III) and significantly greater than species richness under the *Shepherdia/Aster* type. The total mean cover of shrubs in the *Elymus innovatus* community is 13 per cent. The most important shrub component is *Rosa acicularis*, while *Symphoricarpos albus*, *Juniperus communis* and *Shepherdia canadensis* are only rarely present with little contribution to total cover.

The herb, dwarf shrub element of this community is particularly important with 130 per cent total mean cover (Table IV) and is significantly greater ($t = 1.77, p = 0.05$) than herb, dwarf shrub cover the

TABLE II

LOCATION OF STANDS SURVEYED IN JASPER AND BANFF

Stand	Map Ref.	Elevation m	Aspect	Air Photo No.
JASPER				
1	118°.00'W 53°.05'N	1380	NW	5202X 21
2	117°.51'W 53°.12'N	1200	E	19669 62
3	118°.07'W 52°.56'N	1050	SE	5221X 13
4	118°.06'W 52°.54'N	1200	NW	5221X 13
5	117°.57'W 52°.55'N	1350	SW	5221X 16
6	118°.06'W 52°.53'N	1500	N	5219X 8
7	118°.03'W 52°.53'N	1050	SW	5219X 9
8	118°.04'W 52°.48'N	1170	N	5219X 8
9	118°.02'W 53°.03 N	1530	SW	5301X 19
10	117°.44'W 52°.35'N	1280	SW	19670 64
11	117°.44'W 52°.36'N	1260	SW	19670 64
12	118°.03'W 53°.11'N	1200	SW	5304XA 149
13	117°.52'W 52°.39'N	1260	W	19670 79
14	118°.05'W 53°.08'N	1140	NE	5304X 20

TABLE II (Continued)

Stand	Map Ref.	Elevation m	Aspect	Air Photo No.
15	118°.04'W 53°.11'N	1170	S	5304XA 149
16	118°.02'W 52°.51'N	1200	SW	5219X 9
17	118°.02'W 52°.52'N	1140	level	5219X 9
BANFF				
18	115°.25'W 51°.09'N	1410	level	5103X 52
19	115°.26'W 51°.08'N	1380	SW	5103X 52
20	115°.32'W 51°.13'N	1410	E	5105X 22
21	115°.43'W 51°.11'N	1620	SW	5104X 19
22	115°.37'W 51°.11'N	1500	S	5104X 19
23	115°.32'W 51°.12'N	1650	SE	5105X 22
24	116°.48'W 52°.03'N	1650	SW	5203X 49
25	116°.57'W 52°.09'N	1950	SW	5200X 13

TABLE III

SPECIES RICHNESS BY COMMUNITY TYPE

Stand	COMMUNITY TYPE																								
	Elymus innovatus			*Shepherdia/Aster conspicuus*										*Vicia americana*											
	19	1	23	9	24	16	13	7	14	11	6	5	17	21	15	4	22	10	20	18	25	8	12	3	2
Number of species	33	34	35	28	19	25	25	21	25	15	22	24	26	19	21	24	24	23	29	36	18	19	33	35	40
	$\bar{x} = 36$			$\bar{x} = 23$										$\bar{x} = 26$											

Vicia americana type. Herbs common to all stands include *Elymus innovatus, Galium boreale, Hedysarum boreale* and *Smilacina stellata*; those completely absent include *Viola adunca, Mitella nuda, Arnica cordifolia, Epilobium angustifolium* and *Petasites sagittatus*.

The bryoid occurrence and cover in this community type are very small in all stands, with only 0.2 per cent total mean cover. Only *Brachythecium salebrosum* is common to all stands, other species with low prominence values occurring only occasionally in stands of this community type. Soils under two stands are Orthic Eutric Brunisols, and under stand 1 is a Degraded Eutric Brunisol.

Vicia americana Community Type

The twelve stands of this community type have only broad similarities, and are less easily defined relative to stands of other aspen community types throughout the parks. The stands occur over a broad range of elevations (1,000 m - 1,900 m) typically but not exclusively on south or southwest aspects. Member stands of this community type are found in Jasper and Banff. Total mean basal area is greater than that of other community types, but total mean age, canopy cover and density do not differ greatly from other stands. The total mean species richness is intermediate to the two other community types.

The tree canopy and stem density are predominantly *P. tremuloides* with very few individual *P. balsamifera, Picea glauca* or *Pinus contorta* stems. Total mean density of dead *P. tremuloides* is intermediate in the three community types, much more than that in the *E. innovatus* type.

TABLE IV

STRUCTURAL FEATURES OF COMMUNITY TYPES

Synusium	Community type		
	Elymus innovatus	*Spiraea/Vicia*	*Shepherdia/Aster*
TREE*			
Height $\bar{x}$ m	15.1	15.6	14.8
range	12.6 - 17.4	9.6 - 26.1	9.9 - 19.8
Cover % $\bar{x}$	55.6	71.6	74.1
range	46 - 69	47 - 86	53 - 89
Age $\bar{x}$	56	49.4	49.1
range	42 - 75	44 - 61	35 - 62
Density $\bar{x}$	630	1070	1167
Stems/ha r	450 - 830	550 - 2210	640 - 1810
Basal Area $\bar{x}$ m^2/ha	77.3	96.8	83.5
range	73 - 100	63 - 140	53 - 120
SHRUB			
Cover $\bar{x}$	13.2	14.3	14.2
range	8 - 18	2 - 38	2 - 35
HERB			
Cover $\bar{x}$	139.3	99.5	92.8
range	125 - 150	36 - 147	63 - 168
BRYOID			
Cover $\bar{x}$	0.2	0.6	1.8
range	0.1 - 0.3	0 - 2.7	0.3 - 3.3

*Live aspen only.

The total mean cover of shrubs (14.3 per cent) (Table IV) does not distinguish this community type from others. The most frequent component, *Spiraea lucida* is accompanied only by *Rosa acicularis*, which is common to all aspen stands in the parks, and occasional shrubs such as *Viburnum edule, Ribes oxyacanthoides* and *Amelanchier alnifolia*. There is no shrub consistently present in all stands of this community type.

Herbs and dwarf shrubs are relatively less prominent in this community type with a total mean cover of 99.5 per cent. The most important members are *Arctostaphylos uva-ursi, Fragaria virginiana,* and *Vicia americana*, all others occurring only occasionally with less frequency and cover. Most of the less common grasses occur in stands of this community type, including *Festuca subulata, Poa pratense, Koeleria cristata* and *Calamogrostis rubescens*. The cover and frequency of *E. innovatus* are relatively less than in stands of any other community type. Bryophytes and lichens are unimportant in stands of this community type with a total mean cover of 0.5 per cent. *Brachythecium salebrosum* and *Amblystegium serpens* are the major bryoid components.

Soils are all Orthic Eutric Brunisols, except under stand 21 which is a Degraded Eutric Brunisol.

Shepherdia canadensis/Aster conspicuus Community Type

The stands of this community are mainly confined to Jasper Park, where they occur over a relatively narrow elevational range (1,000 m - 1,500 m). Aspect is predominantly southwest, mainly on low angle slopes. This community type has the lowest total mean number of

species (Table III).

The total mean cover (74 per cent) and density (116 per ha.) of trees (Table IV) are the largest of all the community types, while height, basal area and age are all less than in other aspen communities. The mean density of dead aspen greatly exceeds that of other communities. *P. balsamifera*, *Picea glauca* and *Pinus contorta* are relatively unimportant members of the tree overstory.

Total mean cover of shrubs (14 per cent) is the same as that under other communities. The major shrubs, *Shepherdia canadensis* and the ubiquitous *Rosa acicularis* contribute the major portion of the shrub cover, with *Juniperus horizontalis* and *Symphoriocarpos albus* as minor elements.

The total mean cover of dwarf shrubs and herbs is lowest (92 per cent) of all three types in this community. The major contributions to this cover include *Linnaea borealis*, *Lonicera involucrata*, *Lathyrus ochroleucus* and *Aster conspicuus*, with smaller amounts of *Fragaria virginiana*, *Pyrola secunda* and *Galium boreale*. *Elymus innovatus* occupies a position midway between the other two community types. Occasional minor elements, including *Oryzopsis pungens*, *Viola adunca* and *Arnica cordifolia* occur more frequently in stands of this community type.

Bryophytes and lichens, have a higher total mean cover than under any other community type (1.8 per cent), contributed in part by the importance of *Brachythecium salebrosum* and *Amblystegium serpens*, as well as the diversity of species which is greater under some stands of this community type than the other two communities.

Most soils are Orthic Eutric Brunisols, except those under stands 11 and 16, Degraded Eutric Brunisols, and that under stand 24 an Orthic Regosol.

Soils

The soils of the montane zone have been studied in only a few localities to date (Rutter 1965; Hnatiuk 1969; Stringer and La Roi 1970; Dumanski 1970), and classification has been to the sub-group level in most studies.

The soils throughout the parks have in most cases been developed on glacial till deposits, although localized lacustrine, outwash, aeolian and avalanche activity has given rise to peculiar parent materials. Of the twenty-five stands surveyed only eight are located on till deposits. The remainder of the aspen stands are located on lacustrine deposits or at the base of avalanche chutes. In extreme situations a distinct soil profile has not developed and vegetation is supported on rock covered slopes. Textural analysis places all soils in the sandy loams, certain horizons being silt loam, loamy sand or loam. Soil reaction is neutral to strongly alkaline (pH 6.1 - 8.5; Appendix III).

Most soils on drier sites are classified as Orthic Eutric Brunisols. Profile characteristics were not well defined and were generally shallow above heterogenous parent material. Litter accumulation was thin and overlays thicker humus accumulation (mean 9.2 cm) in an Ah horizon. The deepest horizon, Bm, lies directly over deep till

or lacustrine deposits, often with numerous pebbles and angular rock fragments.

In stands, 1, 11, 16 and 21, eluviation of the mineral A horizon, to form a weak Bt below, has resulted in Orthic Luvisols. Overlying parent till, lacustrine or avalanche materials these soils are associated with thinner developed soil profiles.

Stands 24 and 25 occupy steep slopes with platy cleavage quartzites and angular limestones underlying thin organic accumulations. These Orthic regosols, rapidly drained with relatively small quantities of mineral soil, exhibit slow downhill 'creep' as evidenced by tree growth form and distribution.

Soil Moisture Regime

Despite numerous studies of aspen from autecological and physiological viewpoints, very little information exists of the site water relations of aspen. Baker (1925) presented much useful but qualitative information on the site characteristics of aspen in the west. Frequent mention of sites as 'dry', 'moist' or 'well drained' (Kittredge and Gevorkiantz 1929; Stoeckeler 1948; Lynch 1955; and Reed 1971) does not provide any quantitative or comparative information. Warner and Harper (1972) review the subject of aspen site conditions and conclude that little is known related to the soil-plant water relations of aspen or the specifics of site preference for aspen. Precipitation and temperature (as reported from established clima-tological stations in close proximity to the stands) are considered in

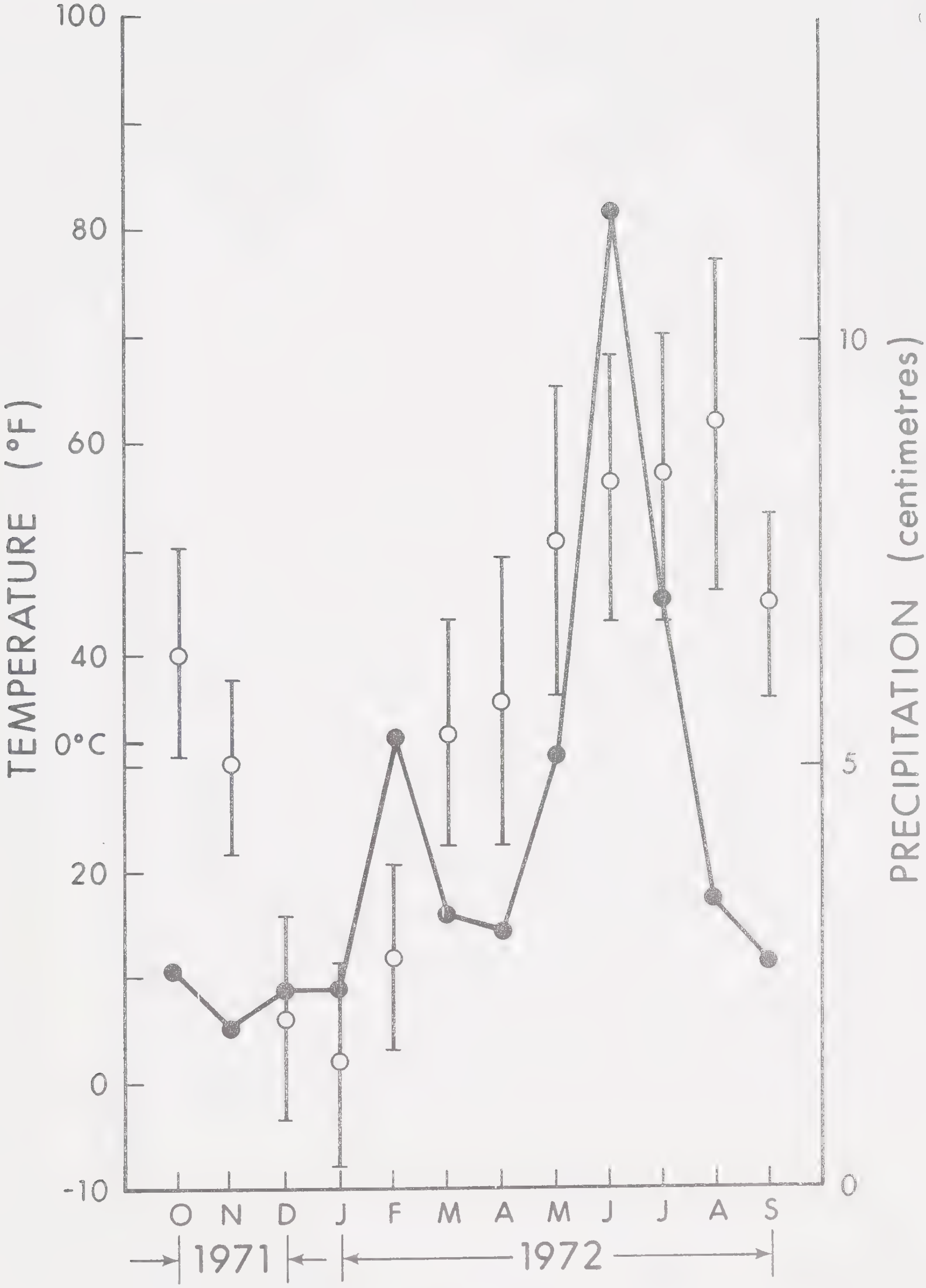
Figure 11 (A, B, C) for each of the three stands 2, 5 and 13. Two of the stations (Jasper townsite and East Gate) report very similar mean maximum and minimum temperatures. The Athabasca Falls station, close to stand 13, reports mean maximum temperatures much the same as the other stations, but lower mean minimum temperatures throughout the year, with greater diurnal temperature range.

Precipitation patterns are similar in all three sites, with maximum snowfall in February and maximum rainfall in June. Stand 13 received 100 per cent more snow than either 2 or 5. Rainfall in 2 during April 1973 exceeded precipitation during the same month in 13 and 5, by 33 per cent and 85 per cent respectively. Total precipitation throughout the period October 1971 to September 1972 was greatest in 13 and least in 5.

Under stands 2 and 13 following snowmelt in March and April, soil moisture content increases to a maximum in April and May at all but the deepest points measured (Fig. 12A, 12C). In these stands there is a greater delay between snowmelt and achievement of the maximum moisture content. A delay between the maximum recorded summer precipitation and soil moisture increase occurs in each of these stands, most pronounced at the 55 to 95 cm depth in stand 13 but less distinct in stand 2. While similar patterns of precipitation and soil moisture content are evident in stand 5 (Fig. 12B), the pronounced delay in soil moisture maxima after spring melt is not evident, and all soil horizons reach maximum moisture content at the same time (May), rather than reflecting sequential infiltration from the surface downward. From July onwards,

FIGURE 11A

Maximum, minimum and mean temperature and mean monthly precipitation at stand 2 (Canada Department of Transport).



TEMPERATURE (°F)
100
80
60
40
0°C
20
0
-10
PRECIPITATION (centimetres)
10
5
0
O N D J F M A M J J A S
1971
1972

FIGURE 11B

Maximum, minimum and mean temperature and mean monthly precipitation at stand 5 (Canada Department of Transport).

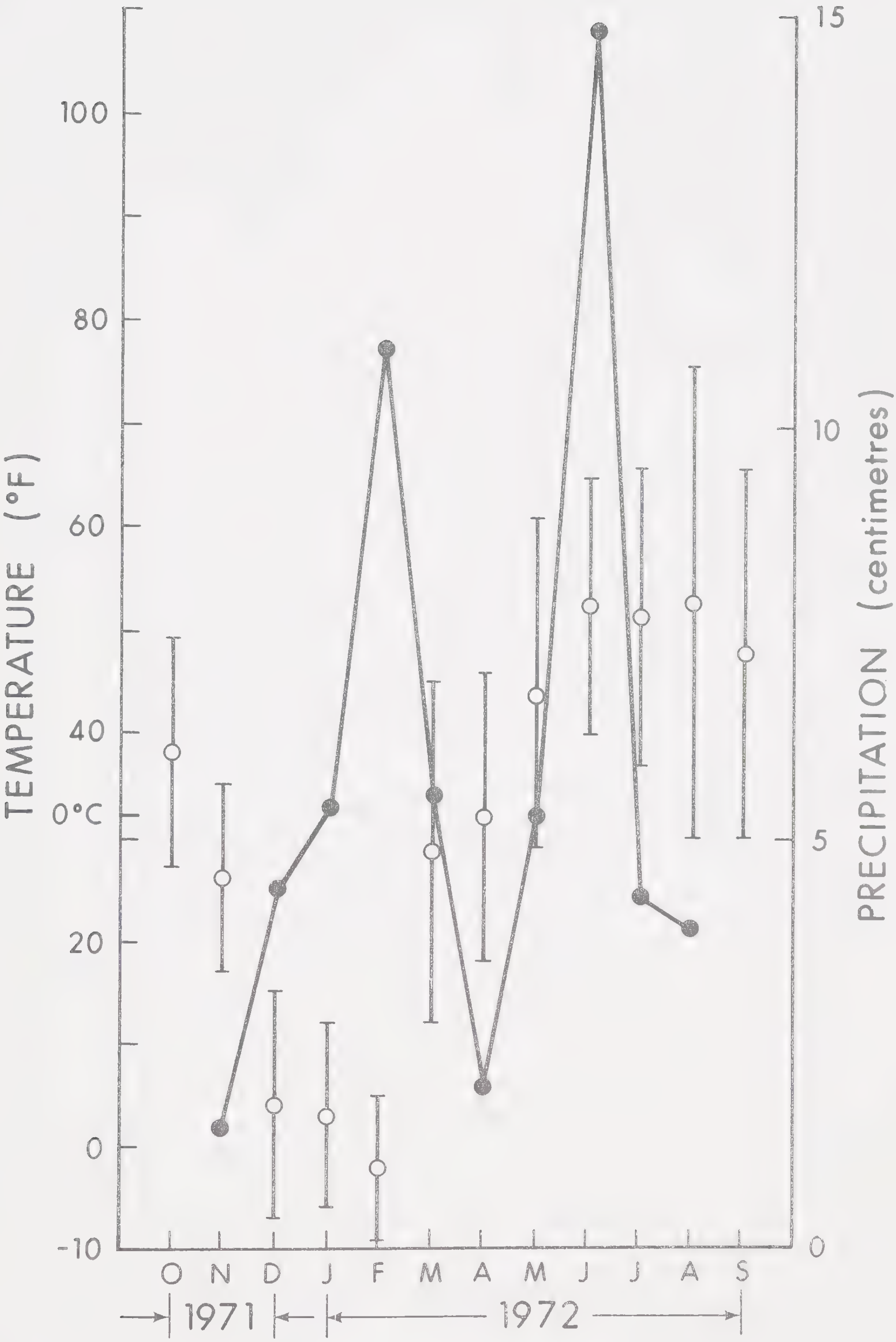

TEMPERATURE (°F)
100
80
60
40
0°C
20
0
-10
PRECIPITATION (centimetres)
15
10
5
0
O N D J F M A M J J A S
1971
1972

FIGURE 11C

Maximum, minimum and mean temperature and mean monthly precipitation at stand 13 (Jasper National Park, Warden Service).

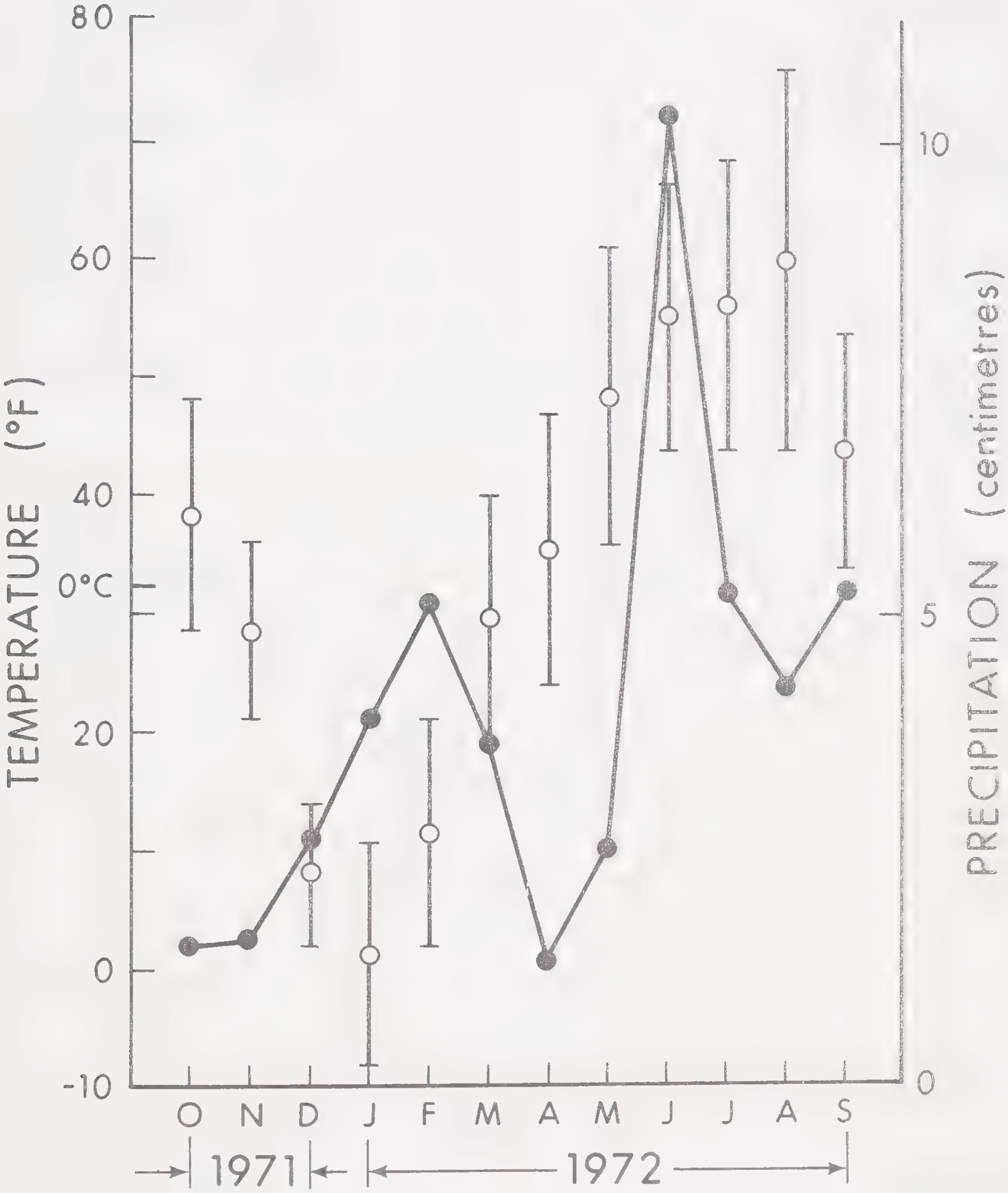

80
60
40
0°C
20
0
-10
TEMPERATURE (°F)
10
5
0
PRECIPITATION (centimetres)
O
N
D
J
F
M
A
M
J
J
A
S
1971
1972

FIGURE 12A

Soil moisture by volume. Stand 2. Means and standard error in Appendix IV.

10 - 50 cm ▲

25 - 65 cm ■

40 - 80 cm ○

55 - 95 cm ●

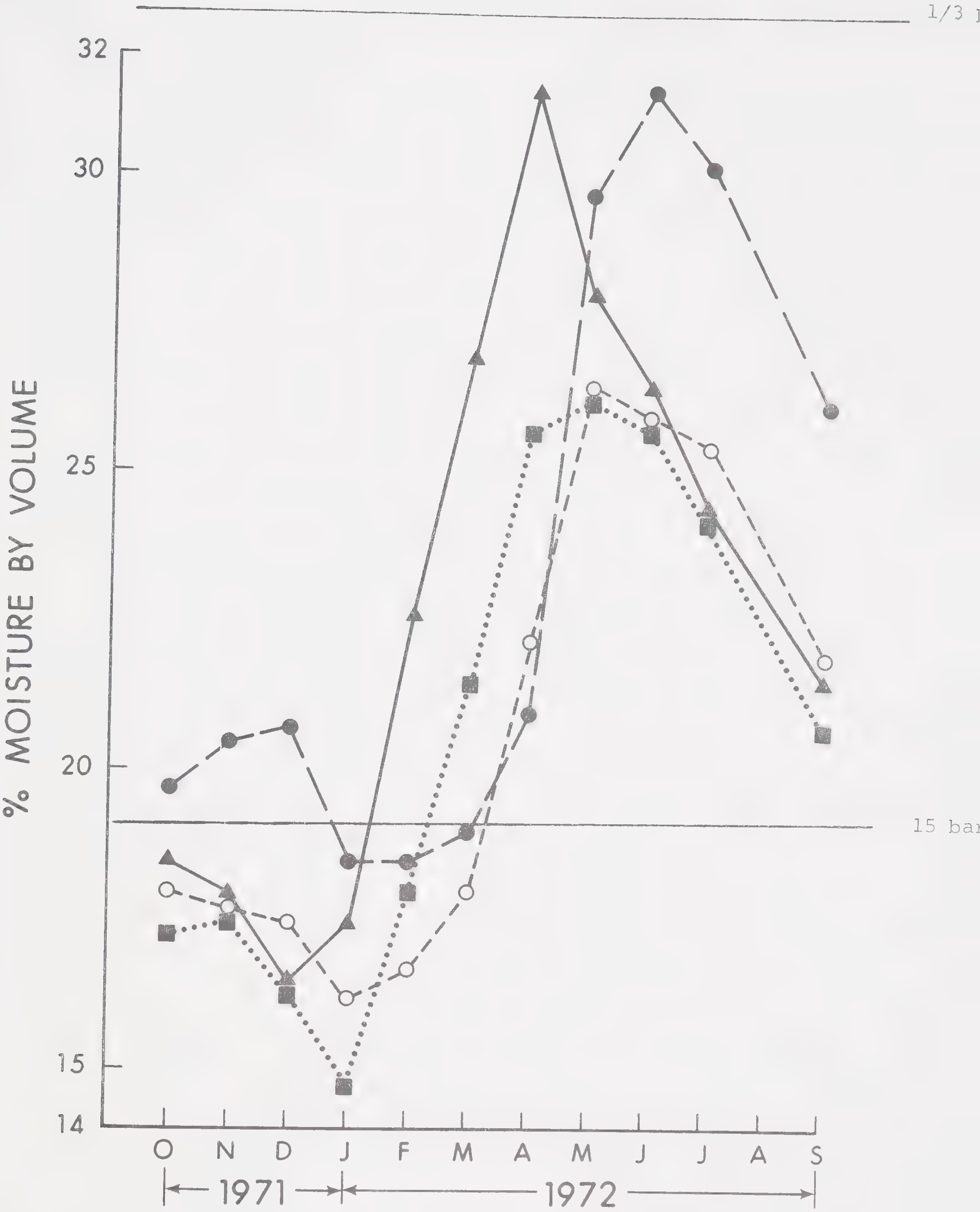
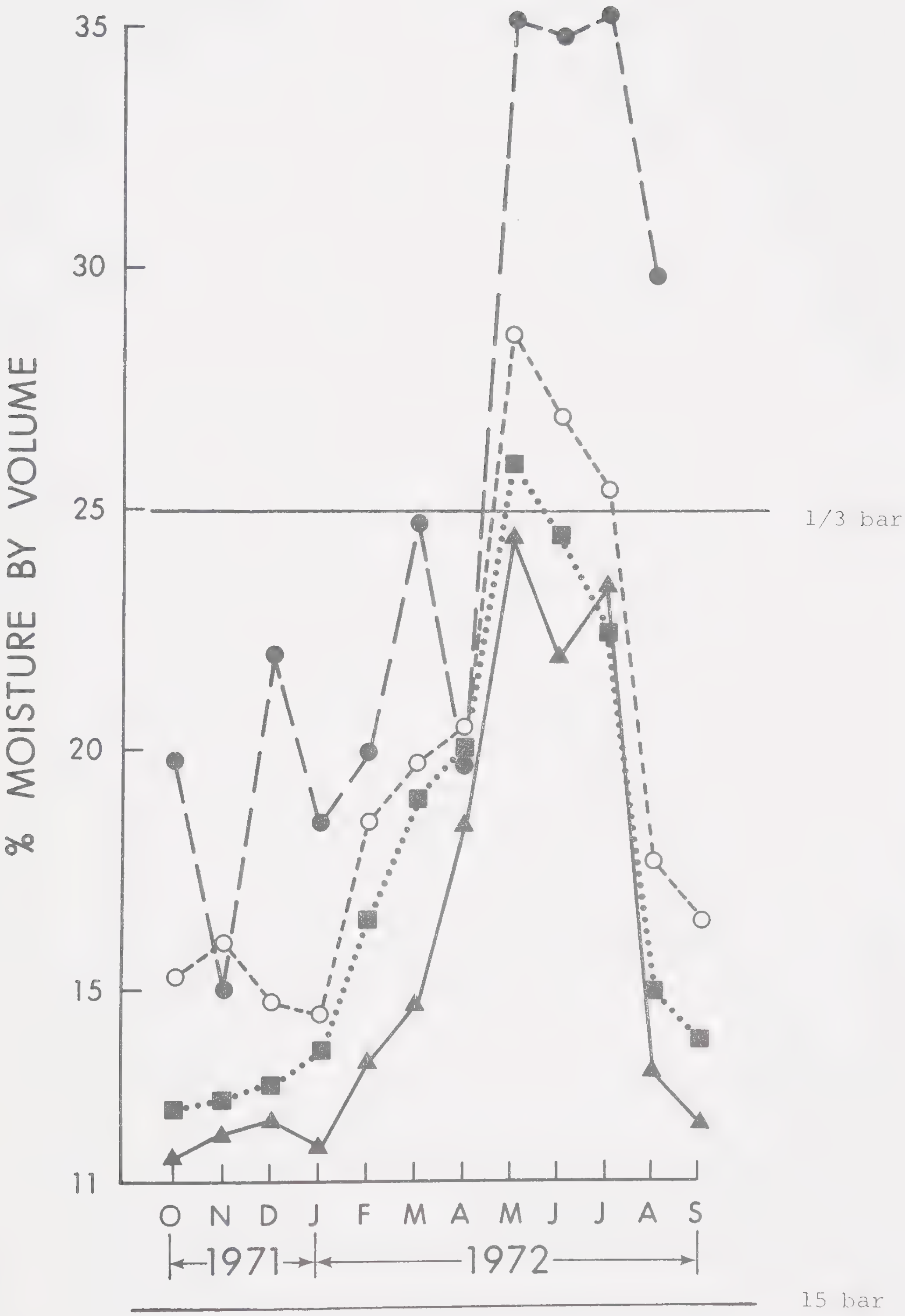

1/3 b
15 bar
% MOISTURE BY VOLUME
32
30
25
20
15
14
O
N
D
J
F
M
A
M
J
J
A
S
1971
1972

FIGURE 12B

Soil moisture by volume. Stand 5. Means and standard error in Appendix IV.

10 - 50 cm	▲
25 - 65 cm	■
40 - 80 cm	o
55 - 95 cm	●



% MOISTURE BY VOLUME
35
30
25
20
15
11
1/3 bar
O N D J F M A M J J A S
1971
1972
15 bar

FIGURE 12C

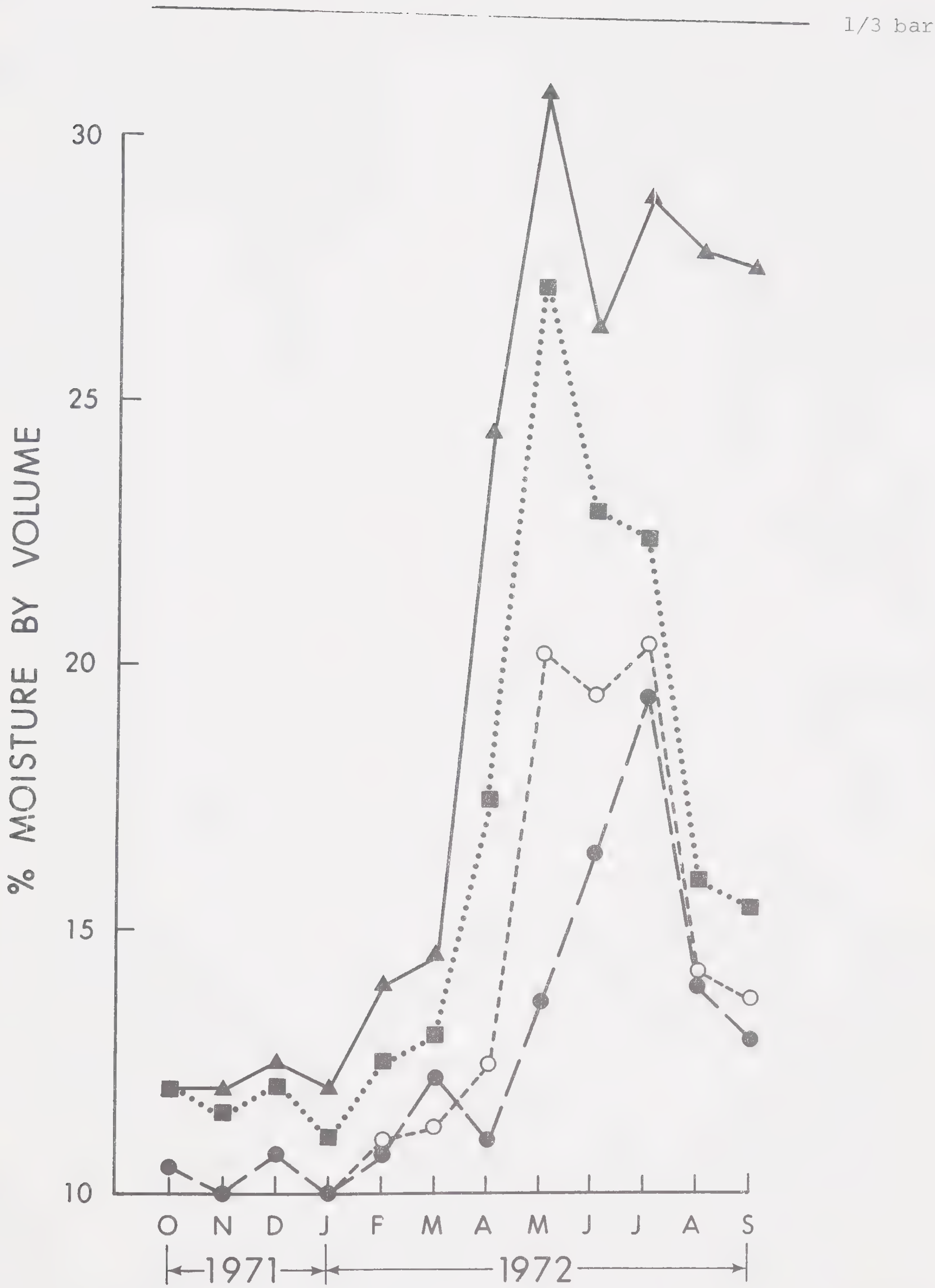
Soil moisture by volume. Stand 13. Means and standard error in Appendix IV.

10 - 50 cm ▲

25 - 65 cm ■

40 - 80 cm ○

55 - 95 cm ●


1/3 bar
30
25
20
15
10
% MOISTURE BY VOLUME
O N D J F M A M J J A S
1971
1972
15 bar

soil water is depleted gradually to minimum values in mid-winter.

The uppermost areas of the soil profile apparently are depleted of moisture most rapidly in stands 2 and 5, while stand 13 retains high moisture at the 10 - 50 cm depth, at least for the annual cycle described. Soil in stand 13 retains moisture in increasingly large volumes from depth to surface respectively. Stand 5 is apparently the reverse situation, inasmuch as at depth moisture content is greatest, and relatively less toward the soil surface. Similar patterns are not evident in soil of stand 2, in which both surface and deep samples retain relatively larger volumes of water than horizons in the middle of the profile.

During the period of investigation, it was noted that stand 5 was situated on an avalanche fan which lay downslope from a deep channel between two mountain peaks. During spring melt, free flowing surface water frequently emerged in a vegetated channel within the stand, but the ephemeral nature of this surface flow made it impossible to tell whether or not sub-surface flow occurred throughout the growing season. Recognizing the lack of quantification of the sub-surface water recharge in stand 5, correlation of soil moisture content with precipitation was tested (Table VI). Correlation was poor for stands 5 and 13, but good for stand 2. The lack of strong correlation may be accounted for in a number of ways, some of which are related to the use of neutron probe techniques for soil moisture measurement. However this method was considered the best available for repeated readings and ease of installation.

TABLE V

MECHANICAL ANALYSIS OF SOIL SAMPLES TAKEN AT THREE DEPTHS FROM STANDS 2, 5 AND 13

Stand	Depth (cm)	Sand %	Silt %	Clay %	Moisture Content (By Weight)		
					Field Capacity -1/3 Bars	Pressure Wilting Point -15 bars	1/3 - 15 bars AV.M %
	0 - 10	66	25	9	34.3	9.5	24.8
13	10 - 20	69	27	3	26.6	7.6	19.0
	20 - 40	53	36	10	35.0	8.0	27.0
	0 - 10	63	29	8	36.2	20.0	16.2
2	10 - 20	53	37	10	36.0	14.7	21.3
	20 - 40	53	35	11	29.1	22.6	6.5
	0 - 10	61	37	2	28.0	9.5	18.5
5	10 - 20	66	32	3	28.6	11.5	17.1
	20 - 40	79	18	5	17.5	7.2	10.3

TABLE VI

SIMPLE CORRELATION COEFFICIENTS BASED ON MONTHLY DETERMINATIONS OF SOIL MOISTURE IN STANDS 2, 5 AND 13 MEASURED BY NEUTRON PROBE, AND MEAN TOTAL MONTHLY PRECIPITATION

$r = 0.63 \quad P \leqq 0.05 \quad r = 0.76 \quad P \leqq 0.01$

Depth (cm)	2	13	5
10 - 50	+0.44	+0.14	+0.40
25 - 65	+0.66*	+0.23	+0.48
40 - 80	+0.79**	+0.33	+0.49
55 - 95	+0.87**	+0.39	+0.58

*Significant correlation at 95%.
**Significant correlation at 99%.

The incidence of rocks and voids near the probe access tubes introduces error into the moisture readings (Holmes 1966; Richardson and Burroughs 1972). The soil chemical composition is important to the accuracy of the probe, calcium being effective in moderating neutrons to give wide responses for soils of the same density and moisture content (Cottechia *et al.* 1968). This may be important in stands on alkaline soils with high calcium content and basic parent materials.

Wetting fronts, transmission zones and any abrupt soil moisture interfaces influence the probe readings (Lawless *et al.* 1963).

Finally, the depletion of soil moisture by evapotranspiration may introduce time-related errors which contributes to the negative or low correlation of soil moisture content with precipitation. Aspen has been shown to deplete total moisture status of sites by as much as 8 per cent (Croft and Monninger 1953).

Significant correlations for precipitation and soil moisture content in stand 2 are not altogether expected when the previous considerations of error for stands 5 and 13 could equally well apply to stand 2. The inherent errors in neutron probe techniques are probably valid for all three stands, but natural features of stand 2 modify the errors previously suggested and provide conditions for positive correlation of soil moisture and precipitation.

No estimates of actual or potential evapotranspiration were made in this study, but soil sand, silt and clay content may indicate the relative moisture regimes under which plants exist in the three stands 2, 5 and 13. Rutter (1968) has compiled information from a number of

studies to show that uptake of water equals the potential transpiration of the plant. Potential transpiration demand is not met when 33 per cent, 50 per cent and 75 per cent of available water has been depleted from clay, loam and sand respectively.

Thus marginally greater clay plus silt content which could reduce potential transpiration under stand 2 may be compensated by greater available water capacity. Overall, less of the available water capacity may be utilized by the vegetation, providing a stronger relationship between precipitation and soil moisture. Higher air temperature are a feature of the area around stand 2, but the setting of the stand on an east facing terrace in the lee of a tall cliff and mountain peak may be important for shading during days when water loss by rapid evapotranspiration is experienced on exposed sites.

The period during which aspen stands undergo soil moisture stress is obviously important to the persistence of the stands on a particular site. Soil moisture stress conditions may also be influencial in determining the physiognomy of the canopy as well as understory vegetation. Previous studies by Schultz *et al.* (1967), Zan (1968) and De Byle *et al.* (1969) concentrated upon soil moisture regime under pure aspen stands in Utah. Moisture measurement was made by neutron probe techniques, and soil moisture reported as inches or centimeters in the upper few feet of the soil profile where aspen roots are concentrated. When spring moisture levels were measured, it was assumed that the soil was close to field capacity (1/3 bar). Expressed as per cent of total soil volume, the results showed field capacity to be between 30 per cent

and 37 per cent. Permanent wilting percentage (15 bars) at which vegetation could be assumed to be under soil moisture stress conditions is not directly reported. However, minimum soil moisture readings in the growing season between 14 per cent and 18 per cent by volume may be close to PWP.

It is clear that the measurements made of field capacity in the Utah studies are very close to measurements made in the Jasper and Banff aspen stands (Table V, p. 73). Although the present study made moisture measurements at field capacity and PWP on a weight basis; the degree of similarity between Utah studies and the present work has provided the basis for estimating 1/3 and 15 bar moisture content for each of the three stands monitored (Figs. 12A, B, C).

Only stand 2 apparently undergos any degree of moisture stress, this mainly during the winter period October to February. Field capacity is exceeded only in stand 5, and was never reached during the growing season of 1971-72 in either stands 2 or 13. The greatest increase in soil moisture above field capacity occurred in the deepest measured points of stand 5.

It would not appear that soil moisture stress occurs over a sufficiently long period during the growing season in any of the aspen stands monitored to affect the physiognomy of the stand. It is, however, possible that the lack of moisture stress in these aspen stands, representative of many more throughout the Parks, is strong reason for the occurrence and persistence of aspen on these sites. The fact that soil moisture exceeds field capacity only in stand 5 may not be

influencial in the community relations aspect of aspen. However, physiognomy of the stand which is remarkably lush in understory cover could well be a result of this plentiful supply of water. The soil moisture conditions certainly accord well with the observation that stand 5 is fed by a stream during early summer.

The three stands selected for study of monthly moisture flux represent two community types, and three site conditions within these types. Stand 2 is established under conditions which are both moist and cool. The level terrace on which the stand grows receives precipitation in amounts equal to that in stand 5, but moisture retention is improved by topographic setting and silt plus clay content of the soil. Broad fluctuations in soil moisture do not occur in stand 2. The lowest points sampled in the profile in stand 2 seem to change as much in moisture content as the top most horizons (14 per cent - 15 per cent between summer and winter). Soil moisture stress probably occurs throughout winter months and very early spring in the lower soil horizons.

Stand 13, exposed on a slope with western aspect receives full mid-day insolation. Winter precipitation is twice that in stands 2 and 5 and summer precipitation 33 per cent greater. The wide fluctuations from winter to summer (12 per cent - 31 per cent) of moisture in the upper soil horizons of stand 13 reflects the dependency on moisture recharge by precipitation. There is no evidence that ground water recharge occurs in this stand. Neither soil moisture stress nor field capacity were achieved in this stand.

The location of stand 5 suggests that the hydrologic regime is dependent upon sub-surface recharge supplemented by precipitation. The summer precipitation is less than that in stands 2 and 13, but during winter, snowfall is equivalent to that in stand 2. Soil moisture shows broad fluctuations from winter to summer, most pronounced in the deepest horizons sampled and least in the uppermost horizons. Spring and early summer stream flow through the stand is considered to be mainly responsible for the soil moisture status in the lower soil horizons, upper horizons reflecting moisture input by precipitation. Soil moisture exceeded field capacity in the growing season, but never went below permanent wilting percentage.

Environmental Relations

The natural complexity of any ecosystem makes direct interpretation of qualitative or quantitative features difficult. The forester, concerned primarily with productivity, may use site index curves derived from height and age data. But when environmental and vegetation features are considered together, it is not uncommon to find that relationships are closely interconnected and not necessarily directly related one to another. Previous studies (Beil 1966; Hnatiuk 1969; Stringer and La Roi 1970; Achuff 1974) have utilized ordination techniques in an attempt to clarify plant-environment relationships. In plotting environmental features on the ordination field conclusions are reached on the influential factors for the vegetation type under review. The same technique is utilized in this work, but the number of

environmental variables is restricted to those showing reasonable correlation (Tabe VII).

The use of simple correlation coefficients is an attempt at a better understanding of plant-environment interactions, although the significant correlation of two variables does not imply a unique relationship between just these two variables. Stringer and La Roi (1970) point out that non-linear relationships between variables are frequently encountered, suggesting that more than one environmental variable may be influencing plant distribution at any one time.

Although the altitude of a stand in the relatively small geographic area of Jasper and Banff Parks may not be directly influential, other environmental features may be closely connected with altitude. A broad subdivision in the ordination field demonstrates that the higher elevations support stands of the *Vicia americana* community type lowest elevations the *Shepherdia/Aster conspicuus* community type, and *Elymus innovatus* community type stands tend to be at mid elevations.

Soil moisture is an important feature, particularly as field capacity at 20 - 40 cm and available moisture capacity at 0 - 10 cm. The ordination is subdivided by these two variables in such a way that a sample of stands in all community types to the right of the field are wet to mesic, those to the left dry to xeric (Fig. 12, p. 66). High available moisture capacity in the upper soil horizons delimits the group of stands to the left of the field. Thus where field capacity is least, available moisture capacity is greatest. Available moisture

TABLE VII

SIMPLE CORRELATION COEFFICIENTS (r) OF THIRTEEN SELECTED VEGETATIONAL AND ENVIRONMENTAL VARIABLES

r = ±0.39 for P = 0.05
r = ±0.49 for P = 0.01

		2	3	4	5	6	7	8	9	10	11	12	13
Total Angiosperm Cover	1	-.28	.19	.14	.22	.94**	-.01	.32	.38	-.29	.17	-.10	-.12
Tree Density (*P. tremuloides*)	2		-.39*	-.11	.02	-.29	-.11	.24	-.46*	.35	.49*	-.32	-.40*
Tree Density (*Picea glauca*)	3			-.15	-.09	.23	.30	.18	.19	-.15	.46*	.42*	.30
Tree Basal Area (*P. tremuloides*)	4				.12	.11	.11	-.02	-.05	-.13	.02	-.04	-.12
Total Shrub Cover	5					-.09	.08	.23	-.11	-.08	.20	.20	.03
Total Herb Cover	6						-.04	.24	.42*	-.27	.10	-.17	-.13
Silt plus Clay at 40 cm	7							.05	-.12	.23	.23	.41*	.48*
Aspect	8								-.01	-.16	-.13	.15	.05
Elevation	9									-.74**	.01	-.03	.38
Available Moisture Capacity at 10 cm	10										.18	.03	-.14
Available Moisture Capacity at 20 cm	11											.45*	.27
Available Moisture Capacity at 40 cm	12												.69**
Field Capacity at 40 cm	13												-

*Significant correlation at 95%.
**Significant correlation at 99%.

capacity influences and subdivides most strongly those stands in the *Shepherdia/Aster conspicuus* community type.

Silt plus clay content of soils have proved particularly useful (Haig 1929; Pluth and Arneman 1965) in describing site conditions, especially as they are related to moisture relations. With increasing depth of sample, the silt plus clay content subdivides stands on the ordination field in various ways. At the 0 - 10 cm depth, stands from all three community types to the left of the field have greater soil silt plus clay content. A similar relationship holds at the 10 - 20 cm sample depth, but at 20 - 40 cm the predominantly high silt plus clay content occurs in stands at the bottom of the field, including the *Elymus innovatus* community type with some stands in the *Shepherdia/Aster conspicuus* community type (Fig. 16, p. 92).

The relationship of phosphorous to stand ordinations is unclear, and poorly defined. Nitrogen does demonstrate a strong subdivision of the ordination field on the X axis, placing stands in all three community types to the right of the field with high N content, stands in the *Shepherdia/Aster conspicuus* and *Vicia americana* community types occur to the left of the field. Other soil chemical attributes were not useful in subdividing the ordination field into environmental trend sectors.

The chosen environmental variables on the ordination field demonstrate two trends within the plant community types already described. Altitude and soil silt plus clay at sample depth of 20 - 40 cm are closely connected with the subdivision of three community

types. Silt plus clay, nitrogen, available water capacity at 0 - 10 cm and field capacity at 20 - 40 cm all subdivide the community types along the X axis of the ordination. The overall impression is that stands to the left of the ordination field are dry to xeric, rich in silt plus clay and low in nitrogen, those stands to the right tending to mesic or wet, higher in nitrogen and less available moisture capacity.

Vegetation Distribution Patterns on the Ordination

The ordination of all twenty-five stands was used to plot various parameters related to the vegetation within each stand. The results of simple correlation were used as a guide in the choice of variables to be plotted on the ordination. Since the bryoid component of all stands investigated was rather poor, no distribution plots of bryophytes or lichens were developed.

The data for vegetation cover and frequency, as plotted on the ordination (Figure 9) and subdivided with supportive evidence from a second selective ordination (Figure 10), described three community types. The placement of these communities was as follows:

In the lower portion of the field, an *Elymus innovatus* community, closely interconnected with a *Shepherdia/Aster conspicuus* community, and in the upper portion of the ordination a *Vicia americana* community.

Tree synusium. The plotted values of aspen density do not coincide well with any other variables either vegetative or environmental. The density of aspen appears to have little connection with

the community types described. The negative correlation with elevation is not clear from the ordination field, but comparison of data does show that the least dense stands are located at the higher elevations.

Stands within the *Shepherdia/Aster conspicuus* and the *Vicia americana* communities are included within two broad categories of high canopy cover (Figure 13). Stands in the centre of the field, and all those in the *Elymus innovatus* community type have relatively less canopy cover. Although canopy cover *per se* was not tested by simple correlation, total angiosperm cover including trees was not significantly correlated with any environmental variables. The highest canopy coverage did coincide with high N (Figure 14) on the ordination field.

The age of aspen stands may be strongly influenced by edaphic characteristics as well as disturbance such as fire and avalanche. The stands are not even-aged by community type, but there is a trend indicating the oldest stands are associated with the *Elymus innovatus* type and some stands on the lower portion of the ordination within the *Shepherdia/Aster conspicuus* community types. An interrelationship exists between age and elevational distribution of the stands (Figure 14). Whether the incidence of disturbance at higher elevations is less than in valley bottoms, is not known although animal grazing and browsing may occur most frequently at higher elevations in the summer. Since any significant difference is unlikely, the age/elevation relationship is considered related more to site conditions than any biotic influence.

Owing to the criteria of choice, few aspen stands had coniferous species growing in the understory. The greatest density of *Picea glauca*

FIGURE 13

Physical characters, tree characteristics and herb prominence values on ordination field. Actual values in Table III and Table VI.

(a) Altitude (metres).

1. 1,000 - 1,199; 2. 1,200 - 1,399;
3. $>$ 1,400.

(b) Density of *P. tremuloides* (stems/hectare).

1. 40 - 60; 2. 61 - 80; 3. 81 - 100;
4. $>$ 100.

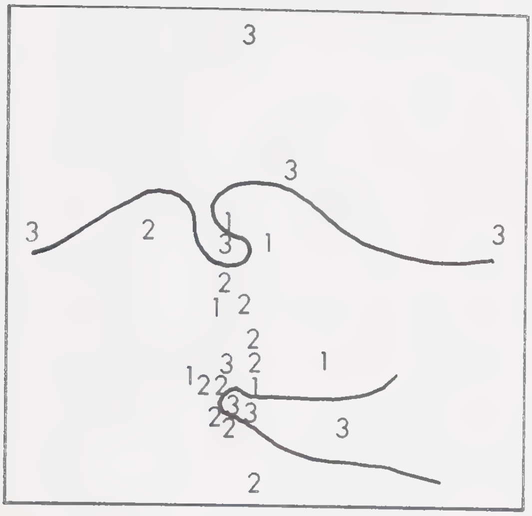
(c) Canopy cover of *P. tremuloides* (%).

1. 40 - 50; 2. 51 - 60; 3. 61 - 70;
4. 71 - 80; 5. $>$ 80.

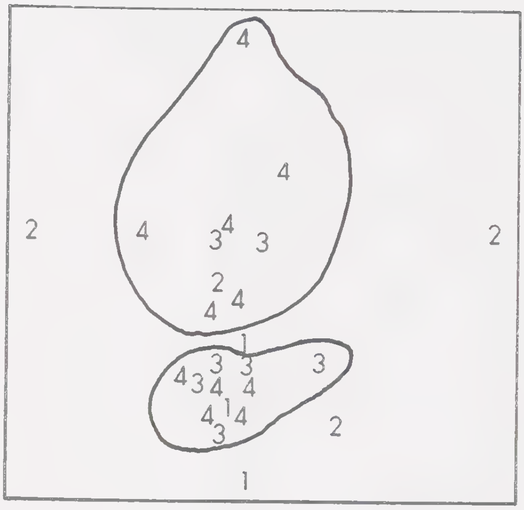
(d) *Elymus innovatus*. Prominence values.

1. 10 - 100; 2. 101 - 200; 3. 201 - 300;
4. $>$ 300.

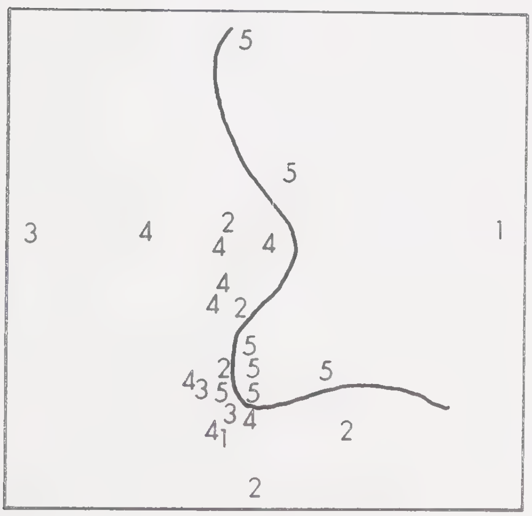
\- No data.



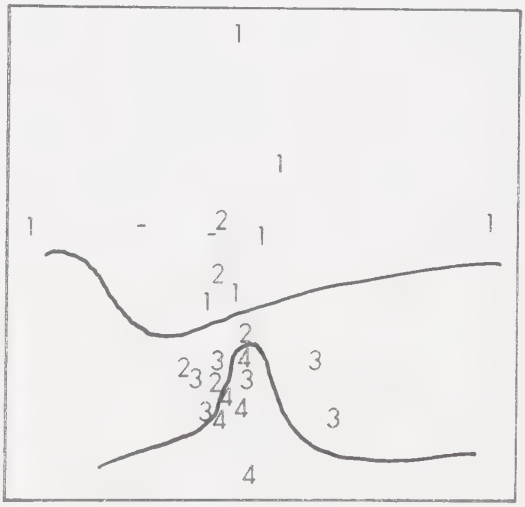
(a)



(b)



(c)



(d)

FIGURE 14

Soil physical and chemical attributes plotted on ordination field. Actual values in Table IV and Appendix III.

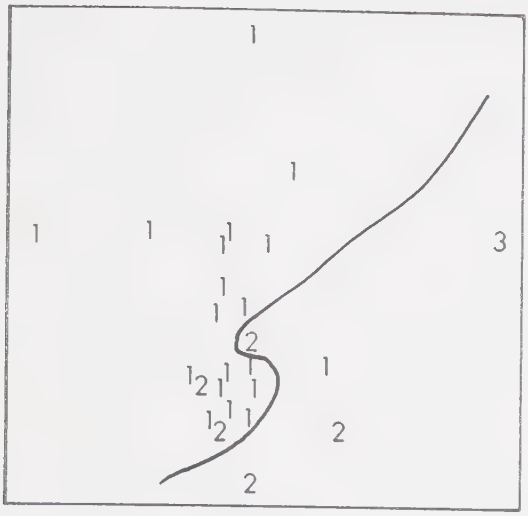
(a) Field capacity (-1/3 bar) at 20 - 40 cm.
1. 5% - 25%; 2. 25% - 45%; 3. 46% - 65%.

(b) Available moisture at 0 - 10 cm.
1. 0 - 10; 2. 11 - 15; 3. 15 - 20;
4. $>$ 20.

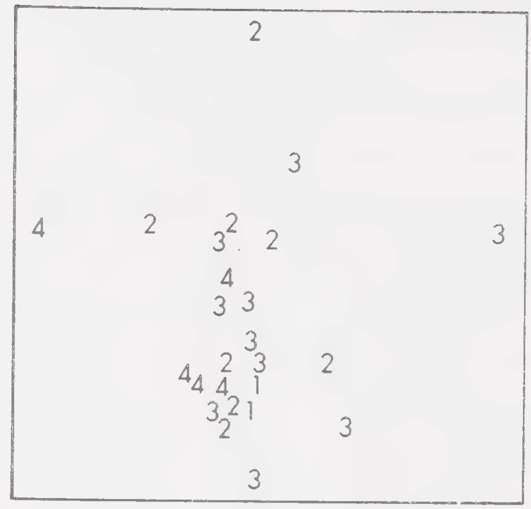
(c) Phosphorus (ppm) at 20 - 40 cm.
1. 1 - 2; 2. 3 - 4; 3. $>$ 4.

(d) Nitrogen (ppm) at 20 - 40 cm.
1. 1 - 2; 2. 3 - 4; 3. $>$ 4.

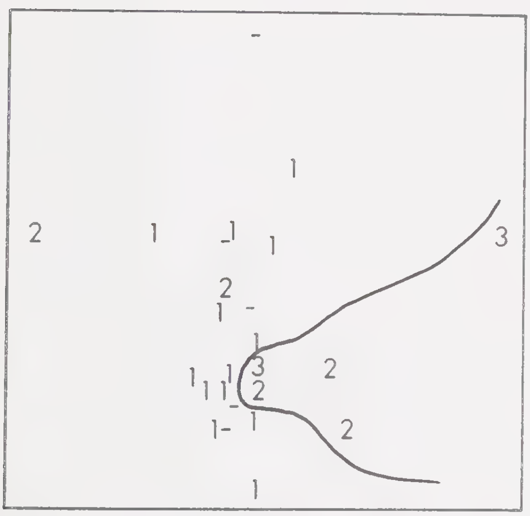
\- No data.



(a)



(b)



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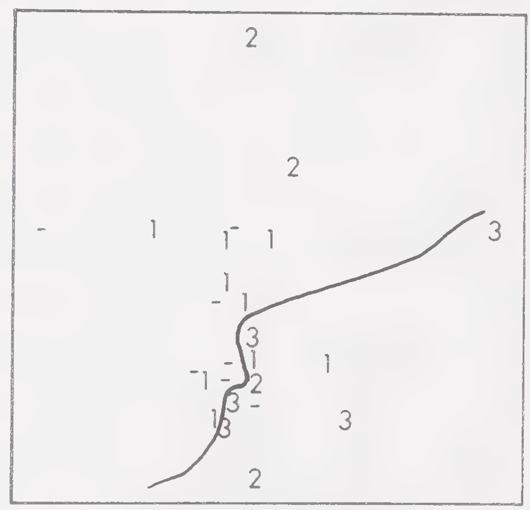

(d)

occurs in the lower left portion of the ordination, within the *Elymus innovatus* community type and one stand from the *Shepherdia/Aster conspicuus* type. A lack of *Picea glauca* or low densities were recorded in the *Vicia americana* community type. This would indicate that the coniferous tree species are distributed over a broad range of sites, but are closely associated with particular understory species, which have been utilized in this study for description of aspen community types. Further clarification is required of the successional trends in understory and tree species of aspen stands in the parks, before the significance of present observations can be judged.

Shrub synusium. The complement of shrubs in each community type is not large either by frequency, density or diversity. Since difficulty was experienced in utilizing most shrub species as indicators of habitat or community type, only two shrubs were eventually plotted on the ordination.

When *Shepherdia canadensis* PV's are plotted in the ordination (Figure 15) the greatest frequency of occurrence coincided with the lower portion of the field, which is to be expected since this is the *Shepherdia/Aster conspicuus* community type. The highest *S. canadensis* PV's are, however, to the left of the field with a close fit to high silt plus clay at 0 - 10 cm (Figure 16) and low nitrogen at 20 - 40 cm (Figure 14). Although no significant correlation is found for shrub cover with any environmental variables, it is clear that *S. canadensis* is associated with sites on which moisture conditions are dependent upon silt plus clay fractions. Available moisture capacity at

FIGURE 15

Shrub and herb prominence values on the ordination field. Actual values in Table III.

(a) *Spiraea lucida* prominence values.

1. 1 - 10; 2. 11 - 20; 3. > 20.

(b) *Vicia americana* prominence values.

1. 1 - 10; 2. 11 - 20; 3. > 20.

(c) *Shepherdia canadensis* prominence values.

1. 1 - 20; 2. 21 - 40; 3. > 40.

(d) *Aster conspicuus* prominence values.

1. 1 - 5; 2. 6 - 10; 3. 11 - 20;
4. > 20.

● No data.

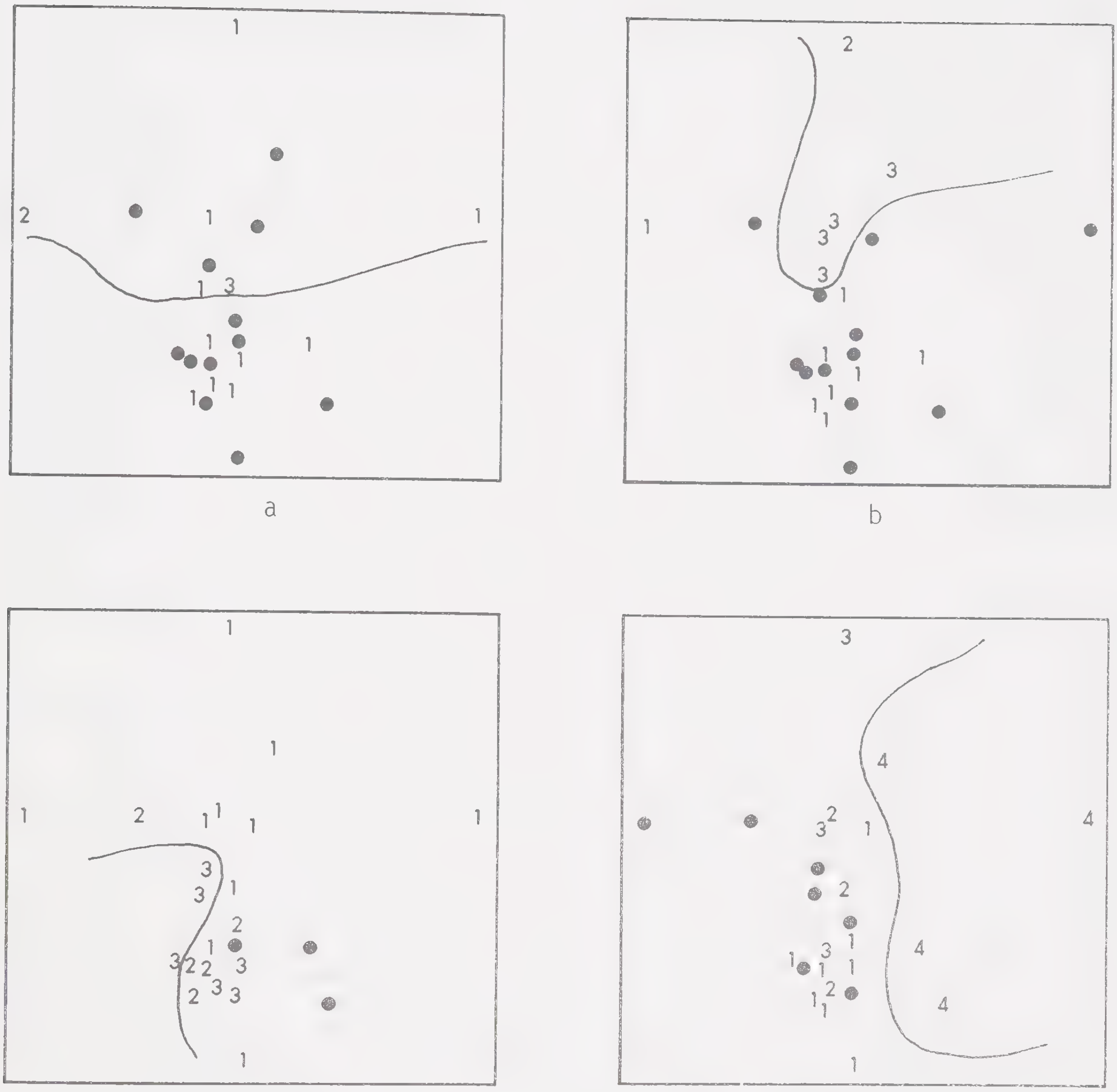
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FIGURE 16

Soil physical attributes on ordination field. Actual values in Appendix III.

(a) Silt plus clay at 0 - 10 cm.

1. 20% - 30%; 2. 31% - 40%;
3. 41% - 50%; 4. > 50%.

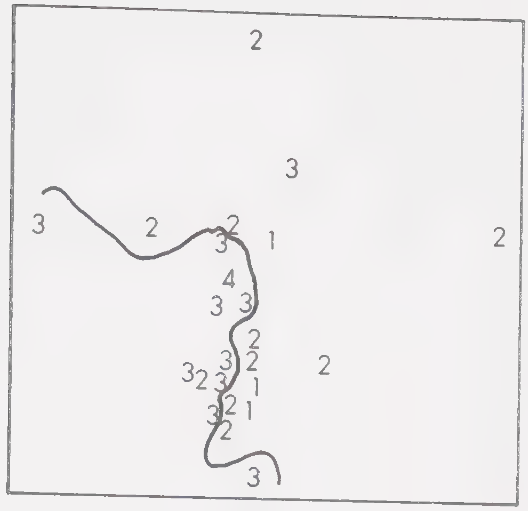
(b) Silt plus clay at 10 - 20 cm.

1. 20% - 30%; 2. 31% - 40%;
3. 41% - 50%; 4. > 50%.

(c) Silt plus clay at 20 - 40 cm.

1. 20% - 30%; 2. 31% - 40%;
3. 41% - 50%; 4. > 50%.

● No data.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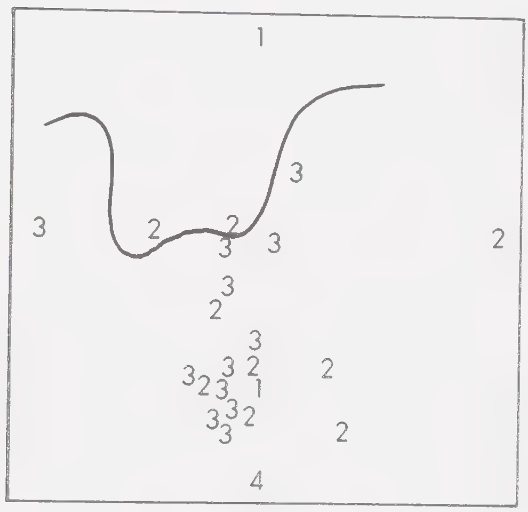
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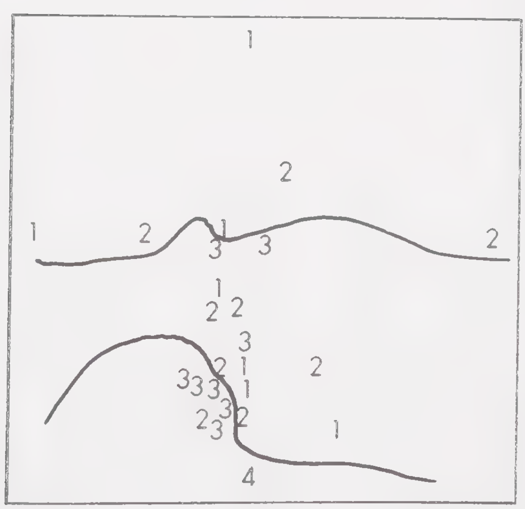
(b)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(c)

0 - 10 cm is higher on the sites occupied by *S. canadensis*.

The incidence of *Spiraea lucida* throughout the three community types indicates the broad range of conditions under which this shrub will grow. Greater PV's in the upper section of the ordination subdivide the *Vicia americana* community from the two others. The pattern of distribution follows higher elevation and low silt plus clay at 0 - 10 cm and 20 - 40 cm. Presumed higher precipitation or extended spring snowmelt at greater elevations may provide required moisture in the stands where field and available moisture capacity (Figure 16) are relatively less than at lower elevation. Elevation and available moisture capacity at 0 - 10 cm are negatively correlated ($r = 0.74$ when $P \geq 0.05$) (Table VII).

Herb/dwarf shrub synusium. The plots of herb and dwarf shrub PV's on the ordination field demonstrate two general trends oriented to the X and Y axes of the ordination. Total herb cover is significantly correlated with elevation ($r = +0.42$ $P \geq 0.05$) although only *E. innovatus* was obviously distributed on an elevational gradient. The highest PV's of *E. innovatus* occurred at the lowest section of the ordination, coincident with the *E. innovatus* community type (Figure 13, p. 85). With increasing distance from this type, *E. innovatus* became less important in the *Vicia americana* community type.

The distribution of *Aster conspicuus* is strongly oriented to the right of the ordination field, in both the *Shepherdia/Aster conspicuus* as well as the *Vicia americana* community types. The best fit of this species with environmental variables occurs for high nitrogen at

20 - 40 cm, low silt plus clay at 0 - 10 cm (Figure 16) and lower available moisture capacity at 0 - 10 cm.

Vicia americana is most important in the upper section of the ordination field, strongly coincident with elevation and lower silt plus clay at 20 - 40 cm (Figure 16).

The distribution of *Viola rugulosa* is very similar to that of *Aster conspicuus*, with highest PV's at the right of the ordination. Occurrence of this species in stands on the left of the field is particularly uncommon, although the distribution is not confined to any one of the three community types. The dwarf shrubs *Linnaea borealis* and *Arctostaphylos uva ursi* show a coincident pattern, with maximum PV's to the left and lower portion of the ordination (Figure 17). Both are distributed throughout the three community types, but not in all stands. *L. borealis* is more restricted to lower elevations than *A. uva ursi*, but both are closely aligned with the high PV's of *S. canadensis*, low nitrogen at 20 - 40 cm and high silt plus clay at 0 - 10 cm characterizes the sites common to all three species. Since higher elevations are correlated with less available moisture capacity at 0 - 10 cm ($r = 0.74$ when $P = 0.05$), it is considered that the reverse holds true at lower elevations especially to the left of the ordination where high silt plus clay provides greater available moisture capacity.

<u>Conclusions</u>. Environmental factors and plant species selected for plotting on the ordination field were considered to be those most clearly demonstrating the patterns existing in the field. Although only simple correlation was carried out between a number of selected

FIGURE 17

Herb and dwarf shrub prominence values on ordination field. Actual values in Table III.

(a) *Mertensia paniculata* prominence values.

1. 1 - 9; 2. 10 - 19; 3. $>$ 19.

(b) *Viola rugulosa* prominence values.

1. 1 - 5; 2. 6 - 10; 3. $>$ 10.

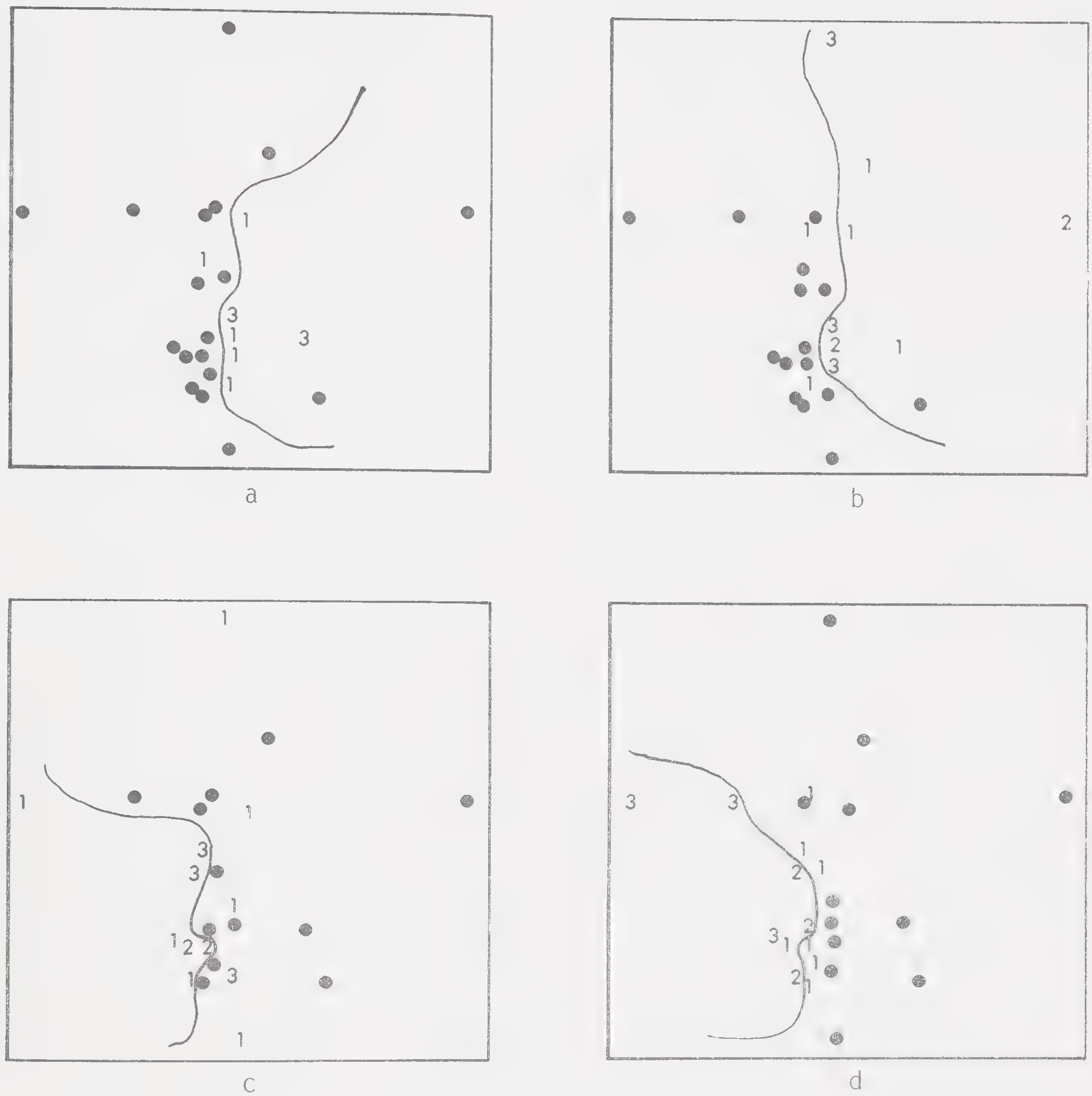
(c) *Linnaea borealis* prominence values.

1. 1 - 20; 2. 21 - 40; 3. $>$ 40.

(d) *Arctostaphylos uva ursi* prominence values.

1. 1 - 20; 2. 21 - 40; 3. $>$ 40.

● No data.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variables, indications are that few environmental and vegetation attributes are strongly correlated. Complex non-linear relationships may be revealed by the use of multiple regression analysis of the data, but the degree to which subjectivity enters into the choice and manipulation of variables for multiple regression was considered inappropriate for the information available.

Three major subdivisions (community types) along the Y axis of the ordination are repeatedly demonstrated with *Spiraea lucida* PV, *Shepherdia canadensis* PV, *Elymus innovatus* PV, *Vicia americana* PV, *Linnaea borealis* PV, elevation, silt plus clay at 0 - 10 cm and silt plus clay at 20 - 40 cm are plotted on the ordination.

Two major subdivisions, cutting across all three community types, are evident on the X axis. Most important features demonstrating this subdivision are *Aster conspicuus* PV, *Viola rugulosa* PV, *Linnaea borealis* PV, *Arctostaphylos uva ursi* PV, *Shepherdia canadensis* PV, *Picea glauca* density, available moisture capacity at 0 - 10 cm, canopy cover, nitrogen and field capacity at 20 - 40 cm and silt plus clay at 0 - 10 cm.

Species prominence values appear to provide more distinct subdivisions along the ordination axes than do soil chemical and physical attributes. Previous work (Achuff 1974) expressed concern for the low correlation of vegetation with environmental variables using soils data. Much of the problem in both this and Achuff's work is ascribed to minimal sampling. Soil nutrient levels were not particularly useful in resolving community or inter-community relationships. Fralish (1972) reports little effect of nutrient levels on aspen growth

in Wisconsin, which may explain the poor correlation of nutrients with aspen and associated understory species distribution. Soil moisture variables and physical soil analyses were, on the other hand, valuable in distinguishing groups of similar stands on the ordination. Aspen site index (site quality) is strongly influenced by soil texture (Fralish 1972), reflects the growth of trees, and is indirectly indicative of understory characteristics. Correlations between vegetation attributes and soil moisture variables, directly related to soil texture, are most commonly obtained in this study, suggesting similar conclusions.

The study of characteristic assemblages of plants (indicators, Clements 1928) in the forest understory, as evidence for site conditions and differences between vegetation types remains a most important part of ecological interpretive techniques. Understory species distributions by community type are thought to be closely allied with patterns of environmental variables. Distribution of aspen communities in Jasper and Banff is likewise dictated by the interrelationship of habitat and vegetation. Comparable information, from studies geographically distinct from those reported here, is required to provide further insight on the site relationships of aspen stands within the Alberta montane zone.

Succession

The subject of forest succession and the occurrence of aspen as a seral species has provided more information in the literature than

any other single subject related to this tree species. Much of the research has been directed toward root suckering response (Sandberg, Dixon and Schneider 1953; Steneker 1974), sucker initiation related to soil types (Stoeckeler 1960) and the invasion of sites through natural succession or after disturbance (Moss 1955; Lutz 1956; Maini 1960 and Bird 1961). Aspen in the central Rocky Mountains has received much attention in the context of successional status and regeneration (Sampson 1916; 1919; Baker 1925; Daubenmire 1943; Hoff 1957; Langenheim 1962; Morgan 1969; Warner and Harper 1972). In western Colorado and central Utah large tracts of aspen with few coniferous seed trees led to the conclusion that aspen was a climax forest type (Baker 1925) although numerous environmental factors at the present time may dictate a successional status for aspen in this area of optimum development. Relatively stable aspen forests are recognized along the western slope of the Rockies and extend into higher altitudes of Utah (Reed 1971). The term 'relative stability' is used, in place of climax, to describe the status of the western slope aspen stands. On the Front Range of Colorado (Marr 1961) southeastern Wyoming (Hoff 1957) and northwestern Wyoming (Reed 1971) subclimax communities are recognized where coniferous growth in the understory is prevalent and understory species diversity is less than that in stable aspen communities. Thus, qualification for climax or stable condition in aspen requires that the species be able to reproduce to the exclusion of other trees capable of dominating the site. The intolerance of aspen to shade (Baker 1925) and the relative tolerance of coniferous species associated with it, provides ideal

situations for the regeneration of conifers under closed aspen canopy. However, as the aspen canopy opens up, either through age or disturbance, conifers can compete with and overtop aspen growth. In the Great Lakes region, aspen stands may begin to deteriorate at thirty-five years (Graham *et al.* 1963). As the trees die or are killed by pathogens, especially *Hypoxylon* canker, few sucker sprouts are produced and those that do come up seldom survive. The land is eventually opened up to shrub invasion.

Morgan (1969) considers inappropriate the application of time scales for Lake States aspen to Rocky Mountain aspen. But even assuming a longer period of time before deterioration of the aspen in the Rocky Mountains, there still exists the possibility that the further away from northern Utah and Colorado, the more likely coniferous species are to succeed the aspen. Although many studies and reports of aspen throughout Canada and the U. S. A. deal with factors causing deterioration of the tree (Graham *et al.* 1963; Maini and Cayford 1968; Davidson and Prentice 1968; Krebill 1972), no one factor is as important to successional trends, as fire. The nature of aspen invasion and succession onto a site can best be followed through an historic sequence.

The pollen record in west central Alberta contains pine and spruce as principal species following glaciation. Aspen pollen is poorly preserved, but aspen undoubtedly played an important part in invasion of Cordilleran forests mainly through the intervention of fire (Hansen 1949). Upon establishment of aspen seed in favourable sites after glacial recession (Baker 1925), disjunct and scattered trees would

have survived in the predominantly coniferous forest cover. In the northern Rockies, *Pinus contorta, Pinus ponderosa* (south of 47°), *Pseudotsuga menziesii* and *Picea glauca* would have been the major needle leafed elements. In the instance of fire, or avalanche in steep mountainous regions, much of the conifer cover would have been burnt or toppled, although as is commonly observed in present day fires, except when very intense, many small islands of trees escape the fire and survive. Immediately the aspens are burnt, root suckering is initiated (Horton and Hopkins 1966). The rapid growth of aspen suckers is independent of site conditions since the parent tree provides initial means of support, which guarantees the dominance of aspen over any conifers which may have seeded onto the disturbed land. Essentially the same sequence of events can take place on an avalanche area, the disturbance turning up new soil for the establishment of seedlings and stimulating aspen to regenerate by suckers. Thus, with the intervention of disturbance, particularly fire which is more influential over large areas than avalanche, aspen is perpetuated, and the rate of conifer invasion is slow where seed trees are relatively few (Morgan 1969). Outside Utah and Colorado, without disturbance of any kind, aspen is succeeded by other species, conifers in the northwest (Morgan 1969), and hardwoods in many parts of the east (Kittredge 1938).

In Jasper and Banff, aspen understory vegetation as already described is subdivided into two general cover types, that dominated by shrubs, with a more open understory on drier sites, and a closed understory dominated by herbs on moist sites. Herb rich understory cover is prominent in stands with the highest percentage canopy cover,

which also coincides with deeper, and nutrient-rich soils. Deeper soils are almost invariably associated with mature aspen growth, rocky soils with conifer overstory (Hoff 1957; Langenheim 1962) or in Jasper and Banff, with rather impoverished aspen stands. *Pseudotsuga menziesii* in Jasper and Banff is considered climax (Stringer and La Roi 1970) while *P. contorta* and aspen are successional dependent upon disturbance. Where *Pinus contorta* seed trees are relatively abundant, direct competition with aspen after disturbance may result in the initial dominance of fast growing aspen ramets eventually overtopped and shaded out by slower coniferous growth. In cool moist sites *Picea glauca* is the climax species, while *P. menziesii* occupies drier rocky outcrops and stony soils (Rowe 1959). Lodgepole pine site has been divided into three phases, xerophytic, mesophytic and moist (Hnatiuk 1969). The mesophytic phase site descriptions and understory characteristics coincide well with those of the *Shepherdia/Aster* community type and the *Elymus innovatus* type. Conditions under aspen stands are apparently suitable to the establishment of pine and white spruce, but Douglas fir is only likely to occupy the driest sites where aspen would possibly not thrive long after disturbance. Some measure of the importance of aspen under Douglas fir is given by Stringer and La Roi (1970). They demonstrate that aspen has the least density of all trees under Douglas fir canopy, with a high mortality much due to animal browse and bark stripping.

Aspen under lodgepole pine does not form an important part of the canopy or understory. Minor differences in site and soil dictate the distribution of individual aspens throughout the pine stands (Hnatiuk 1969).

No information exists of *Picea glauca* forest composition in Jasper and Banff, although from reports of white spruce elsewhere (Steneker 1963; Achuff 1974) and personal observation, aspen is distributed throughout the forest, as individual trees or small clonal groups, assuming a less important part of the canopy as the spruce matures.

Evidence of conifer regeneration under aspen in the parks is available (Table VIII) although no sapling or seedling age data accompanies the density estimates. Highest density of stems for aspen suckers and *Picea glauca* seedlings occur under *Elymus innovatus* community type stands, the oldest stand investigated (1) with greatest density of aspen suckers and spruce seedlings. Whether stand deterioration sets in around seventy years and the canopy opens up cannot be substantiated from this study.

The most striking feature of the aspen stands is the relative lack of regeneration by coniferous species, particularly *Pinus contorta*, and the equally low values of aspen suckers. No quantitative evaluation of browsing was conducted, but observations indicate that animal activity was not a prime cause for the lack of suckers. However, suckers have been observed to be heavily pruned back. Under conditions of rapid sucker production and moderate browsing activity, aspen can regenerate successfully (Krebill 1972).

The present status of the aspen dominated stands therefore appears to be successional in most locations throughout the parks. Where suckers are growing, they will presumably survive to fill the canopy

TABLE VIII

REGENERATION OF SUCCESSIONAL SPECIES UNDER ASPEN CANOPY STANDS ARRANGED ACCORDING TO COMMUNITY TYPE

Stand	Age	Number of Stems/Hectare		
		P. tremuloides	*Picea glauca*	*Pinus contorta*
*1	75	9	9	-
19	42	5	2	-
*23	51	5	1	-
2	51	4	1	-
*3	61	-	1	-
8	44	-	-	3
10	47	-	-	-
12	49	5	-	1
15	49	4	-	-
18	46	4	1	-
20	57	-	1	-
21	40	-	-	-
22	42	3	-	-
*25	50	1	-	-
*5	46	-	1	-
6	62	-	-	1
7	57	-	-	-
9	37	7	3	-
11	43	4	-	-
13	35	3	-	-
14	55	-	-	-
16	62	3	-	-
*17	47	4	-	-
*24	47	1	-	-

*Stands known to have up-slope groundwater recharge.

gaps developing as old trees die. However, the sucker growth is invariably associated in the stand with coniferous seedling growth. The paucity of conifers at the age which some stands have already achieved suggest that the aspen stands will not be succeeded within the next twenty years. From the species distribution (Table VIII), white spruce will be the major successional and presumably climax species on aspen sites in the future, except where particularly dry conditions prevail conducive to lodgepole pine or Douglas fir. Any fires in the aspen stands are expected to be light, and may be a particularly strong stimulant to aspen sucker initiation. Throughout the lodgepole pine and Douglas fir forest, aspen is not expected to be particularly important after light fires, but intense disturbance may bring about an increase in the distribution of aspen stands.

Since white spruce requires shade and a moist mineral soil surface (Le Barron and Jemison 1953) for establishment, and few stands present both conditions, spruce is not likely to invade aspen quickly. Pine will be similarly slow since plentiful seed is guaranteed after fire which releases seeds from cones. Otherwise, seed availability is dependent upon small rodent activity and wind dispersal of seed.

This study agrees with Reed (1971) that the aspen stands are relatively stable at this time, but not climax, at least within Jasper and Banff. Further disturbances will be required to perpetuate the drier site aspen stands, particularly those of the *Shepherdia/Aster conspicuus* and *Vicia americana* type. The *Elymus innovatus* type may regenerate more quickly, and also may present more favourable

conditions for white spruce establishment, which species unlike *P. contorta* does not rely heavily upon fire for seed dispersal. The predominance of aspen or spruce under the *Elymus innovatus* type will be entirely dependent upon the intervention of fire.

Graham *et al.* (1963) point out that the rate of establishment and succession of coniferous species under aspen is dependent in part on site conditions. Thus drier poor sites may take longer to go into a coniferous phase. Although there is no particular support for the rate of succession in the present work, if the statement of Graham *et al.* (1963), holds true for Jasper and Banff aspen stands, the driest sites may not regenerate to aspen, nor become dominated by coniferous growth either pine or Douglas fir. An open phase may develop until disturbance by fire takes place.

To summarize, aspen holds a subclimax position to Douglas fir and white spruce in the parks. Fire and soil disturbance are the major contributing factors to perpetuating aspen. While aspen in the parks does not seem to be rapidly reproducing by suckers, stand age has in all cases surpassed the age of deterioration as given for Lake States aspen (Graham *et al.* 1963). The future of the aspen stands therefore appears to lie in disturbance by fire. Without such intervention, aspen stands may decay to create an open phase without successional species growing from the understory during aspen decline. The forest canopy will be filled eventually by lodgepole pine on drier sites and white spruce in moist sites, the scarcity of Douglas fir in the parks making it unlikely that seed sources will be close enough to senescing aspen stands.

Relationship and Applicability of Other Studies

The diverse and controversial nature of ecological field methodology creates some problems in deriving comparisons between studies af aspen dominated forests. Some studies have been concerned with the vegetation features, some with environmental and vegetation relationships and very few with moisture relations as they may be related to plant cover. Thus comparative statements that follow are primarily based upon characteristics of vegetation, in most cases upon a qualitative basis.

The Alberta prairie distribution and composition of aspen forest is well documented by Moss (1955) and Bird (1961). Moss (1955) considers *P. tremuloides* to be a consociation of the poplar association. He describes five strata or synusiae including the tree canopy. This structure is a great deal more complex than that of the Jasper and Banff stands, and differs especially in having an almost continuous stratum of taller herbs, obscuring taller shrubs during the latter part of the growing season. Although Moss does not subdivide the aspen consociation, species common to the prairie regions include *Symphoricarpos albus, Sherpherdia canadensis, Cornus canadensis, Maianthemum canadense, Rosa acicularis, Viburnum edule, Aster ciliolatus, Vicia americana, Lathyrus ochroleucus, Viola rugulosa, Calamagrostis canadensis* and *Pylaisiella polyantha*. The prairie aspen community would, therefore appear to support species common to both the *Shepherdia/Aster conspicuus* and *Vicia americana* types of the mountains. The incidence of *Aralia nudicaulis* and *Disporum trachycarpum* in central Alberta, but their relative rarity

in northwestern Alberta (Moss 1955) is particularly interesting in view of their occurrence in a number of stands of community types within the mountains. Absent from any list of species given by Moss is *Elymus innovatus*, although *E. glaucus* is prominent in the Cypress Hills aspen. The weight of evidence would seem to be that species common to the prairie aspen association have entered into the montane flora of the mountain aspen communities, while a few Cordilleran species e. g. *Spiraea lucida, Arnica cordifolia, Arctostaphylos rubra* and *Elymus glaucus* have reached areas outside the mountains.

Bird (1961) does not subdivide the aspen poplar community, but considers it a climax forest type in the prairie regions characterized in the understory by species already cited from Moss (1955). In addition, Bird (1961) notes the frequency in the prairie community of *Brachythecium,* the most common moss in montane aspen stands. Emphasis is placed upon the complexity of aspen community understory in the prairies. Unlike aspen stands in the mountains, those in the parkland (Bird 1961) and stands of the *P. tremuloides* consociation (Moss 1955) throughout Alberta have strongly developed herb, dwarf shrub and shrub strata. The shrub stratum is particularly evident in and around successional or recently disturbed stands.

Range surveys in Teton County, Wyoming, (Beetle 1961) described one community and two distinct aspen site types, one on moist sites and the other on dry sites, the site types not mutually exclusive to hillsides or level terrain. Unfortunately, no community classification is suggested but understory species appear to follow the moisture trend.

Common shrubs in the moist sites, *Rosa arkansana, Salix scouleriana, Symphoricarpos albus* give way to *Amelanchier alnifolia, Juniperus communis, Prunus melanocarpa,* and *Shepherdia canadensis* in drier locations. Herbaceous plants exhibit similar peak distributions; common on wet sites are *Agropyron subsecundum, Elymus glaucus,* and *Geum macrophyllum,* giving way to *Agropyron trachycaulum, Calamogrostis rubescens, Agoseris glauca, Campanula rotundifolia* and *Smilacina stellata* with increasingly xeric situations. Common herbs, *Hackelia floribunda, Lithospermum rudeale, Achillea lanulosa, Mertensia ciliata, Hedysarum boreale* and *Castilleja spp,* not attributed to any particular site, bear only passing resemblance to herbs found in Jasper and Banff aspen stands. Grasses and sedges are only a minor element in the understory composition (Beetle 1961). The occurrence of *E. glaucus* on wet sites is similar to the occurrence of *E. innovatus* at lower attitudes in Jasper and Banff on sites with greater available water capacity. The wet-site aspen in Wyoming corresponds best with the *E. innovatus* community types, while the dry site aspen is related to the *Shepherdia/Aster conspicuus* type.

A detailed synecological study of aspen in the Wind River Mountains of Wyoming (Reed 1971) recognizes a single stable *P. tremuloides/ Symphoricarpos oreophilus* association. Association is used in the sense of similar stand groups (*sensu* Daubenmire 1968) and all land areas supporting the same association are one habitat type. This terminology coincides closely with community types and site types as used here.

The Wind River stands are composed of a rich mixture of shrubs, grasses and herbs forming a continuous cover. The foliar overlap creates

a complex understory structure, with total cover exceeding 100 per cent in all but two stands. Shrubs *Symphoricarpos oreophilus, Berberis repens* and *Rosa woodsii*, with *Amelanchier alnifolia* are common in all stands. Major occurring herbs include *Achillea millefolium* (in both), *Rosa woodsii* and *Rosa acicularis, Aster perlegans* and *Aster conspicuus, S. oreophilus* and *S. albus*. The *P. tremuloides/S. oreophilus* association is affiliated with the *Shepherdia canadensis/Aster conspicuus* community type, with some elements common to those of the *V. americana* type. Reed (1971) noted the occurrence of *Arctostaphylos uva ursi* and *Juniperus communis* on heavily grazed sites. In Jasper and Banff these same species are associated with dry exposed sites, both under and outside aspen canopy.

Soil descriptions are given for typical profiles throughout the Wind River stands. No classification was given the soils, but judging by the acidic nature of the profile and parent materials, Dystric Brunisols prevailed. The fertility of these soils was relatively high for the area. Exchangeable K and pH were the only two soil variables available for comparison with the Jasper and Banff stands, and in the case of pH, Wyoming values were appreciably lower. Potassium values were very similar. Parent materials may be largely responsible for this difference. Topography as well as parent material is suggested as responsible for the distributional pattern of aspen in the Wind River Mountains. Similar conclusions are reached for aspen in Jasper and Banff. The nature of the results provides a comparative measure with Alberta montane aspen forests. The Wyoming stands were distributed over

only 300 m elevational range compared with Jasper and Banff stands which occurred over 900 m. Aspen in the Wind River Mountains has fewer suitable sites for colonization and is consequently developed only as one association in a narrow elevational belt with some understory species ecologically equivalent to species in the Alberta montane stands. There is substantial evidence for the similarity of the Wind River association with only one of three community types in Jasper and Banff.

The quality of site for aspen growth has been assessed using understory indicator species (Warner and Harper 1972). Work conducted in Utah and Arizona does not include community classifications, but the dominant shrub, *Shepherdia oreophilus*, suggests a community type analagous to that found in the Wind River Mountains (Reed 1971). Herbs are the most important component in the understory of all stands investigated, and include *Lathyrus lanszwertii*, *Elymus glaucus*, *Vicia americana*, *Poa pratensis*, *Achillea millefolium*, *Smilacina stellata* and *Mertensia arizonica*. The rich herb layer, and occurrence of certain herbs equivalent to those in Jasper and Banff suggests a commonality with the *Shepherdia/Aster conspicuus* type, tending towards the *Elymus innovatus* type. Higher site quality was indicated by the occurrence of *Elymus spp*, *Lathyrus spp* and *Viola spp* in both Utah and Alberta stands.

Ellison (1954) working in the Wasatch Plateau, Utah, provides detailed descriptions of vegetation type, topography and soils. Aspen, common to the montane forest, is represented on southerly exposures in small stands, below steep slopes dominated by tall shrubs including *S. oreophilus*. The impression gained from the descriptions is one of

shrub communities on well drained drier sites upslope from shallow moist slopes dominated by aspen. Ellison (1954) emphasizes that "the occurrence of major plant communities in the subalpine zone are determined principally by topographic factors" -- (which presumably influences soil moisture patterns) -- "and the local climates associated with them. Soil parent material is evidently of minor importance".

Lynch (1955) describes a *Populetum/Symphoricarpetosum* association as common throughout the aspen groveland of Glacier County, Montana. *Symphoricarpos albus* dominates the shrub layer, with *Rosa acicularis, Amelanchier alnifolia* and *Berberis repens* associated. Herbs in this association include *Lathyrus ochroleucus* and *Calamogrostis rubescens, Vicia americana, Achillea millefolium, Fragaria virginiana, Aster conspicuus* and *Smilacina stellata*. The *Shepherdia/A. conspicuus* community type appears to be closely associated in species composition, and physiognomy, with more distant relations to the *V. americana* type. *Populetum Asteretosum* and *Populetum Osmorhizetosum* associations (Lynch 1955) bear little resemblance to stands in Jasper and Banff but are possibly affiliated with aspen dominated stands in Waterton National Park (Kuchar 1975).

In mountain areas of Colorado and Wyoming Costello (1944) investigated range forage types, and clearly identified aspen communities dominated in the understory by *S. oreophilus,* but information on species in undisturbed sites is lacking making it difficult to compare results with these from the Alberta montane.

Langenheim (1962) reports an homogeneous aspen community type

throughout the Crested Butte Area of Colorado. Luxuriant undergrowth dominated by herb species including *Thalictrum fendleri, Vicia americana, Lathyrus lencanthus, Elymus glaucus* and *Osmorhiza occidentalis*. Shrub species were poorly represented, which suggests little relationship to the community types of Jasper and Banff. However, the site conditions in which the Colorado understory species develop have an affinity with the conditions common to the more moist Alberta montane stands, especially those at lower elevations, with *Viola rugulosa* and *Mertensia paniculata* prominent in the understory. Neither of these, nor closely related species occurred in the Colorado stands, but soil and site descriptions are very similar. Aspen in Gunnison County, Colorado, including the area studied by Langenheim, is predominantly herb rich in the understory. Shrubs were most prominent in the Kebler pass area, *Symphoricarpos utahensis* predominant (Morgan 1969). Quantitative soils information demonstrates the acidity of soils under these stands, higher phosphorus than Jasper and Banff soils and a remarkable lack of potassium, possibly due to parent material. Textures included more sand fraction than Alberta montane soils. Aspen soils were distinguished from spruce fir or grassland by organic matter content, nutrient, and especially high or low available moisture capacity.

The east slope of the Front Range in Colorado (Marr 1961) is subdivided into forest climax regions, analagous to elevational zones (Rowe 1959). Aspen occurs in the upper montane (2,500 m - 3,000 m) and the subalpine (3,000 m - 3,500 m). In both zones, aspen dominated sites varying from mesic to xeric, reflected mainly in the growth form and

vigour of the trees. Specific stand descriptions from subalpine sites includes one in which the stand "is close to a small creek and may have a higher water table than the (adjacent lodgepole) pine stand". The understory of the aspen stand is herb rich and lush. Finally, climatological data related to this stand is obviously not sufficient evidence to account for vegetation characteristics, as Marr states "(this stand) may be more mesic -- due to ground water movements that produce the small creek". Although no comparative ground hydrology data is presented, understory species include *Achillea lanulosa, Taraxacum officinale, Fragaria ovalis, Calamagrostis canadensis* and *Poa pratensis* which suggest moist conditions similar to some of the aspen stands in Jasper and Banff. Certain species in the Colorado assemblage e. g. *Poa pratensis, Taraxacum officinale* and *Epilobium angustifolium* suggest a disturbed habitat.

Studies by Hoff (1957), Florez and McDonough (1974) and Baker (1925) cover specific aspects of aspen synecology, and provide only cursory information of understory flora. Herbs and grasses are dominant understory components in Colorado, Wyoming (Hoff 1957) and northern Utah (Florez and McDonough 1974) but in central Utah *S. oreophilus*, dominates the understory (Baker 1925).

Finally, Stoeckeler (1960) investigated soil factors as related to aspen growth in the Lake States. Soil texture, silt plus clay, proved most important in affecting site index (site quality) as a result of increased moisture retention. Where shallow water tables occurred, site index was "substantially increased especially on sandy

soils -- of rather poor water storage capacity".

Conclusions

Aspen dominated forest from southern Utah to northern Wyoming, including Colorado, is predominantly characterized in the understory by shrub, herb and dwarf herb synusiae, the major shrub in all areas being *Symphoricarpos oreophilus*. Some stands, particularly those on the east slopes of the Rockies are reported to lack the shrub synusium. (Hoff 1957; Stoeckeler 1960; Florez and McDonough 1974). Forest stands of the *Thuja heterophylla Pachystima mysinites* habitat type in northern Idaho include *P. tremuloides*, as a seral species following fire. *Pinus ponderosa* is associated with *Symphoricarpos albus* on more xerophytic sites, particularly on southerly slopes (Daubenmire and Daubenmire 1968). The prairie regions of Montana and Alberta aspen grove communities, are often dominated in the understory by *Symphoricarpos albus*, especially near the drier grass and forest ecotone. The aspen within Jasper and Banff lacks *Symphoricarpos* dominance in the shrub synusium. *Shepherdia* and *Spiraea* act as ecological equivalents to *Symphoricarpos* in those stands where shrubs are a dominant feature, which suggests more favourable habitats for these two former shrubs in the montane aspen than for *Symphoricarpos*. There may also be drainage and moisture features which restrict the distribution of *Shepherdia canadensis* outside certain mountain or prairie habitats, since this species is only reported in prairie stands by Moss (1955) and in the Bighorn Mountains by Despain (1971). From observations in Jasper and Banff, and the

foregoing references, *Shepherdia* is associated with the driest sites available. The prominence of shrubs in understory of aspen stands throughout the northwest of America has been emphasized in all the studies reviewed, but herb rich understories gain less prominence. Where species lists and site conditions are available from the same study (Ellison 1954; Langenheim 1968; Morgan 1969; Warner and Harper 1972) it is evident that herbaceous understories are closely associated with moist sites. This agrees with observations in Jasper and Banff. In certain instances, pictorial support to reports (Morgan 1969) or written descriptions (Ellison 1954) confirm that aspen stands are often located below steep terrain or in the downslope drainage of gullies and alluvial fans. This coincides with observations for some stands in Jasper and Banff. These same stands are all predominantly herbaceous in understory cover. The representative of this herbaceous type (stand 5) demonstrated a water regime throughout one annual cycle indicative of subsurface recharge and the opposite of the other two stands studied in which water recharge was purely through the surface from precipitation. Daubenmire (1943) clearly showed that vegetation zonation in the Rocky Mountains was determined by soil drouth, and that topography was important in the distribution of vegetation, telescoping (Daubenmire's terminology) one zone into another. Further work (Daubenmire 1968) expounded on the evidence for each member of the forest series being limited at it's lowest elevation by above-average moisture for that elevation. "Shallow rooted trees" (with which aspen may be identified) "finding their limits on north facing slopes or

where supplies of water lie near the surface".

Aspect, as already demonstrated, is of little direct importance in the distribution of aspen in Jasper and Banff but may be influencial on the site moisture relations of each aspen stand. The distribution of aspen dominated forest, over a broad elevational range, is moisture dependent. Certain understory species are prominent in the very moist habitats *V. rugolosa, M. paniculata* and the very dry habitats, *S. canadensis, A. uva ursi, L. borealis* occurring with aspen in any one of the three community types previously described. The degree of prominence depends upon the relative position of the stand in the landscape and the environmental conditions prevailing within the stand. Species prominence has provided a basis for subdividing the aspen stands studied into three community types, which are related to other gradients than moisture alone. The community types are part of a successional trend, while the subdivision across community types of moist and dry sites is dependent upon soil structure, water recharge systems and topography.

SUMMARY

In the montane zone (Rowe 1959) of Jasper and Banff National Parks, aspen dominated forests are a prominent feature. Frequently occurring as, pure-canopy stands on alluvial fans, river terraces and glacial till deposits, aspen contrasts sharply with surrounding coniferous forest. Topography, soils and disturbance are thought to strongly influence the distribution of these stands.

Numerous stands throughout the parks were identified and briefly surveyed during 1970. Of these, twenty-five were selected for vegetation, soils and moisture analyses. Construction of ordinations (Bray and Curtis 1957) and cluster analyses (Pritchard and Anderson 1971) based upon species prominence values (Beals 1960) demonstrated the existence of three community types as follows: *Elymus innovatus*, *Shepherdia canadensis/Aster conspicuus* and *Vicia americana*. The shrub synusium was evident but not prominent in all three community types. A further subdivision of the three community types was demonstrated by plotting vegetation and environmental variables on the ordination. Without regard to community types, *Shepherdia canadensis* and *Arctostaphylos uva ursi* were shown to be most prominent on dry sites, while *Viola rugulosa* and *Mertensia paniculata* were distributed most frequently in mesic sites.

Elevational criteria were important to the subdivision of community types, as were soil field capacity and silt plus clay at 20 - 40 cm depth.

Subdivision into mesic and xeric sites was found to be related to available moisture in upper horizons and silt plus clay content, in addition to soil moisture recharge phenomena.

Soil moisture was measured over a period of twelve months, in three stands, of differing physiognomy and topographic location. Of the three stands, Number 13 receives 100 per cent more snowfall in the winter, is associated with lower mean minimum temperatures in the winter and shows the longest delay between snowmelt and moisture increases at the lowest points sampled in the soil profile. All stands show soil moisture depletion from July onwards, most slowly in the stand where greatest precipitation is received (Fig. 11, p. 60; Fig. 12, p. 66).

Stand 2 on a level alluvial terrace in the lee of a tall peak is shaded from strong mid-day insolation, which may be important to the conservation of soil moisture through relatively less evapo-transpiration than in stands 5 and 13. Stand 5 is downhill of a deep cleft between mountain peaks, and is known to receive spring runoff in an adjacent stream. The strong fluctuations of soil moisture in lowest horizons sampled and least fluctuations in the surface soil is thought to reflect the recharge from the shallow water table. Those stands receiving water by stream recharge, most frequently on alluvial fan on gully locations, are herb rich in the understory and lack strong development of a shrub synusium.

Aspen stands studied throughout 1971-1972 did not show any soil moisture stress conditions during the growing season, based upon estimates of PWP from moisture by weight analyses and other studies in

Utah aspen stands. However, field capacity as a measure of water abundance was never reached in two stands, but was exceeded in stand 5 presumably due to stream recharge into the stand. It is supposed that aspen is not subject to soil moisture stress conditions at any time in the growing season, unlike other vegetation types growing in close proximity to aspen. The abundance of moisture in aspen soils may influence the understory characteristics and tree physiognomy.

Other studies of aspen throughout North America, particularly the western Rocky Mountains, demonstrate the stability or climax condition of aspen in Colorado or Utah, but on moving away from this centre of 'optimum' development the transgressive and subclimax nature of this forest type. Shrub and herb synusiae are well developed under aspen south of Jasper and Banff. *Symphoricarpos spp.* are particularly important as understory components in aspen outside the parks, but *Shepherdia canadensis* and *Spiraea lucida* appear to be more prominent within the Alberta montane aspen. *Shepherdia* is considered an ecological equivalent to *Symphoricarpos*, in the context of Jasper and Banff.

The 'stability' of aspen is dependent upon the abilities to regenerate. In Jasper and Banff aspen is not regenerating vigorously, nor are successional coniferous species prominent in the understory. Evidence is presented suggesting that aspen is subclimax in the parks to white spruce on moist sites, lodgepole pine or Douglas fir on dry sites. However, the incidence of disturbance by fire has been low since the establishment of the parks, and aspen has not been stimulated to regenerate vigorously by suckers nor is there any evident reproduction

by aspen seed. Although no quantitative evidence is shown as for the level of browsing pressure in aspen stands, it is suggested that whenever aspen suckers do emerge, elk and deer severely prune back the shoots. It is concluded that without the intervention of fire, as aspen deteriorates through old age, drier sites will open up possibly to a shrub phase until conifer seeds are introduced. Moist sites will deteriorate more slowly and may support a mixture of white spruce and some aspen. Fire intervention is necessary for the perpetuation of the aspen forests within the parks.

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APPENDICES

APPENDIX I

Dissimilarity matrix for ordination of twenty-five stands, generated from prominence values of all vascular and non-vascular species. See text for methodology.

Stand	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	0.588	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	0.839	0.673	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4	0.828	0.728	0.828	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	0.337	0.523	0.821	0.765	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6	0.391	0.554	0.864	0.534	0.297	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7	0.548	0.503	0.764	0.546	0.538	0.458	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8	0.754	0.590	0.815	0.443	0.746	0.482	0.509	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9	0.432	0.572	0.849	0.722	0.274	0.399	0.435	0.696	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
10	0.771	0.599	0.807	0.582	0.695	0.509	0.591	0.437	0.692	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11	0.505	0.424	0.818	0.585	0.431	0.381	0.330	0.491	0.357	0.556	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12	0.644	0.574	0.675	0.725	0.606	0.707	0.460	0.643	0.531	0.666	0.531	-	-	-	-	-	-	-	-	-	-	-	-	-	-
13	0.511	0.437	0.814	0.582	0.433	0.363	0.348	0.507	0.353	0.525	0.106	0.581	-	-	-	-	-	-	-	-	-	-	-	-	-
14	0.430	0.454	0.876	0.773	0.275	0.390	0.501	0.751	0.232	0.736	0.368	0.578	0.358	-	-	-	-	-	-	-	-	-	-	-	-
15	0.726	0.657	0.833	0.708	0.491	0.687	0.588	0.698	0.514	0.657	0.581	0.501	0.597	0.601	-	-	-	-	-	-	-	-	-	-	-
16	0.336	0.512	0.761	0.683	0.289	0.362	0.352	0.641	0.237	0.696	0.314	0.488	0.319	0.271	0.591	-	-	-	-	-	-	-	-	-	-
17	0.509	0.668	0.751	0.799	0.413	0.533	0.504	0.754	0.394	0.725	0.480	0.522	0.483	0.392	0.636	0.361	-	-	-	-	-	-	-	-	-
18	0.856	0.800	0.888	0.595	0.804	0.847	0.690	0.765	0.755	0.797	0.734	0.754	0.708	0.804	0.765	0.735	0.822	-	-	-	-	-	-	-	-
19	0.192	0.615	0.821	0.779	0.300	0.376	0.548	0.741	0.341	0.722	0.478	0.602	0.466	0.383	0.639	0.319	0.454	0.786	-	-	-	-	-	-	-
20	0.885	0.793	0.800	0.754	0.682	0.829	0.844	0.858	0.753	0.825	0.830	0.755	0.831	0.783	0.654	0.823	0.791	0.790	0.871	-	-	-	-	-	-
21	0.857	0.834	0.796	0.796	0.750	0.848	0.809	0.853	0.773	0.703	0.830	0.730	0.802	0.814	0.709	0.779	0.695	0.784	0.764	0.646	-	-	-	-	-
22	0.791	0.742	0.895	0.830	0.691	0.757	0.742	0.792	0.658	0.738	0.712	0.681	0.715	0.695	0.635	0.718	0.715	0.779	0.721	0.735	0.408	-	-	-	-
23	0.287	0.586	0.806	0.770	0.252	0.360	0.508	0.722	0.245	0.670	0.435	0.559	0.422	0.344	0.594	0.283	0.421	0.762	0.178	0.769	0.754	0.687	-	-	-
24	0.387	0.578	0.843	0.758	0.371	0.301	0.357	0.624	0.383	0.650	0.411	0.618	0.412	0.397	0.701	0.295	0.371	0.855	0.390	0.856	0.771	0.756	0.358	-	-
25	0.893	0.842	0.891	0.874	0.844	0.891	0.869	0.882	0.856	0.897	0.845	0.816	0.864	0.840	0.858	0.857	0.695	0.899	0.892	0.838	0.740	0.874	0.852	0.691	-

APPENDIX II

Dissimilarity matrix for ordination of selected stands generated from prominence values of all vascular and non-vascular species. See text for methodology.

Stand	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	19	22	23
2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	0.673	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4	0.728	0.828	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	0.523	0.821	0.765	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6	0.554	0.864	0.534	0.297	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7	0.503	0.764	0.546	0.538	0.458	-	-	-	-	-	-	-	-	-	-	-	-	-
8	0.590	0.815	0.443	0.746	0.482	0.509	-	-	-	-	-	-	-	-	-	-	-	-
9	0.572	0.849	0.722	0.274	0.399	0.435	0.696	-	-	-	-	-	-	-	-	-	-	-
10	0.599	0.807	0.582	0.695	0.509	0.591	0.437	0.692	-	-	-	-	-	-	-	-	-	-
11	0.424	0.818	0.585	0.431	0.381	0.330	0.491	0.357	0.556	-	-	-	-	-	-	-	-	-
12	0.574	0.675	0.725	0.606	0.707	0.460	0.643	0.531	0.666	0.531	-	-	-	-	-	-	-	-
13	0.437	0.814	0.582	0.433	0.363	0.348	0.507	0.353	0.525	0.106	0.581	-	-	-	-	-	-	-
14	0.454	0.876	0.773	0.275	0.390	0.501	0.751	0.232	0.736	0.368	0.578	0.358	-	-	-	-	-	-
15	0.657	0.833	0.708	0.491	0.687	0.588	0.698	0.514	0.657	0.581	0.501	0.597	0.601	-	-	-	-	-
16	0.512	0.761	0.683	0.289	0.362	0.352	0.641	0.237	0.696	0.314	0.488	0.319	0.271	0.591	-	-	-	-
19	0.615	0.821	0.779	0.300	0.376	0.548	0.741	0.341	0.722	0.478	0.602	0.466	0.383	0.639	0.319	-	-	-
22	0.742	0.895	0.830	0.691	0.757	0.742	0.792	0.658	0.738	0.712	0.681	0.715	0.695	0.635	0.718	0.721	-	-
23	0.586	0.806	0.770	0.252	0.360	0.508	0.722	0.245	0.670	0.435	0.559	0.422	0.344	0.594	0.283	0.178	0.687	-
Total	9.743	13.720	11.584	8.426	8.479	8.720	10.707	8.106	10.878	7.899	10.108	7.924	8.585	10.574	7.834	9.027	12.411	8.421

APPENDIX III

Soil Mechanical and Chemical analyses by sample depth. See text for methodology.

Stand	Sample Depth (cm)	% Sand	% Silt	% Clay		% Moisture Content -1/3 bars	-15 bars	Available Moisture Capacity %	N ppm	P ppm	K ppm	pH	Conductivity mmhos
1	0-10	51	42	78	100	32.5	13.5	19.0	6.5	1.0	66.5	7.9	0.4
	10-20	49	43	9	100	29.8	11.0	18.8	1.0	2.0	62.0	8.3	0.3
	20-40	46	42	12	100	36.0	12.2	23.8	2.5	0.5	36.5	8.1	0.3
2	0-10	63	29	8	100	36.2	20.0	16.2	5.5	2.5	110.0	7.6	0.1
	10-20	53	37	10	100	36.0	14.7	21.3	8.0	0.5	67.5	8.0	0.3
	20-40	53	35	12	100	29.1	22.6	6.5	4.5	1.0	65.0	8.0	0.3
21	0-10	68	24	8	100	36.0	16.8	19.2	7.5	1.5	78.5	6.7	0.3
	10-20	57	24	19	100	24.6	13.0	11.6	8.0	1.5	70.0	8.2	0.2
	20-40	66	25	9	100	18.0	3.0	10.0	4.0	0.5	51.0	8.2	0.3
25	0-10	65	31	4	100	57.3	38.1	19.2	3.5	29.5	93.5	7.2	0.3
	10-20	63	32	5	100	50.6	30.1	20.5	6.0	21.0	83.0	7.5	0.3
	20-40	63	31	6	100	47.0	24.1	22.9	8.0	19.0	78.5	7.6	0.3
24	0-10	-	-	-	-	79.5	61.0	18.5	0.5	9.0	145.0	7.2	0.3
	10-20	63	32	4	100	40.0	20.6	19.4	2.5	2.0	81.5	7.8	0.3
	20-40	70	24	6	100	35.1	18.8	16.3	7.5	2.5	83.0	7.8	0.3
14	0-10	64	31	5	100	13.1	11.1	2.0	1.5	9.0	146.5	6.1	0.3
	10-20	83	15	2	100	29.0	6.5	22.5	1.5	6.5	46.5	7.7	0.3
	20-40	73	22	5	100	21.0	7.5	13.5	2.5	2.5	47.5	7.9	0.3
5	0-10	61	37	2	100	28.0	9.5	18.5	0	27.5	363.5	8.1	0.5
	10-20	66	31	3	100	28.6	11.5	17.1	0.5	2.5	85.0	8.2	0.2
	20-40	79	18	3	100	17.5	7.2	10.3	0.5	5.5	73.0	8.2	0.3
17	0-10	68	21	11	100	22.8	9.3	13.5	0	9.5	130.5	7.2	0.3
	10-20	64	22	14	100	24.0	11.0	13.0	0.5	2.0	103.0	7.7	0.2
	20-40	62	24	14	100	24.5	9.1	15.4	1.0	2.5	112.5	8.3	0.2

Stand	Sample Depth (cm)	% Sand	% Silt	% Clay		% Moisture Content -1/3 bars	-15 bars	Available Moisture Capacity %	N ppm	P ppm	K ppm	pH	Conductivity mmhos
6	0-10	71	22	7	100	9.5	5.5	4.0	1.0	33.5	57.5	7.2	0.3
	10-20	66	21	13	100	18.3	5.8	12.5	0	6.5	39.5	7.3	0.3
	20-40	63	21	16	100	20.6	5.8	14.8	0	1.0	36.5	7.5	0.3
15	0-10	68	23	9	100	22.0	7.5	14.5	0.5	50.5	234.0	7.2	0.2
	10-20	65	19	16	100	17.8	5.6	12.2	0	4.5	106.0	7.2	0.2
	20-40	77	18	5	100	12.5	7.5	5.0	0	2.0	53.5	8.2	0.2
13	0-10	66	25	9	100	34.3	9.5	24.8	0	1.0	98.0	8.2	0.1
	10-20	69	27	4	100	26.6	7.6	19.0	1.5	0.5	67.5	8.3	0.1
	20-40	53	36	11	100	35.0	8.0	27.0	1.0	1.0	70.0	8.4	0.1
22	0-10	53	41	6	100	27.5	9.1	18.4	2.0	1.0	151.5	7.5	0.4
	10-20	52	45	3	100	20.5	7.1	13.4	5.5	0	48.5	8.1	0.2
	20-40	55	40	5	100	16.3	5.1	11.2	1.0	0	30.0	8.5	0.3
23	0-10	63	30	7	100	50.1	36.3	13.8	5.5	2.5	148.5	7.7	0.3
	10-20	57	33	10	100	27.8	9.8	18.0	4.5	0.1	103.0	8.0	0.4
	20-40	55	29	16	100	23.6	8.1	15.5	4.5	0	105.5	8.3	0.4
20	0-10	66	22	12	100	23.5	11.0	12.4	2.0	0.5	99.0	7.9	0.3
	10-20	70	22	8	100	20.3	9.3	11.0	2.5	0.5	86.5	7.9	0.1
	20-40	75	20	5	100	17.5	7.3	10.2	3.5	0	71.5	8.3	0.2
10	0-10	42	38	20	100	30.5	8.0	22.5	0.5	6.0	55.5	6.8	0.2
	10-20	50	32	18	100	26.8	6.1	20.7	0.5	3.0	47.0	7.7	0.2
	20-40	79	11	10	100	6.9	6.1	0.8	0.5	3.5	41.0	8.2	0.3
16	0-10	56	29	15	100	31.1	12.6	18.5	0.5	1.5	173.0	6.7	0.5
	10-20	54	29	17	100	24.5	10.3	14.2	0.5	2.0	153.5	6.6	0.3
	20-40	67	24	9	100	24.1	11.2	12.9	0.5	2.0	202.0	8.0	0.3

Stand	Sample Depth (cm)	% Sand	% Silt	% Clay		% Moisture Content -1/3 bars	% Moisture Content -15 bars	Available Moisture Capacity %	N ppm	P ppm	K ppm	pH	Conductivity mmhos
19	0-10	64	34	2	100	20.8	8.6	12.2	9.0	0.5	66.5	8.0	0.4
	10-20	54	42	4	100	22.8	7.5	15.3	3.5	0	51.0	8.3	0.3
	20-40	50	44	6	100	25.5	6.3	19.2	5.0	0	68.0	8.5	0.3
18	0-10	52	46	2	100	30.8	10.3	20.5	4.0	0.5	37.5	3.0	0.3
	10-20	59	34	7	100	27.6	9.0	18.6	1.5	0.5	61.0	8.1	0.3
	20-40	75	19	6	100	15.3	6.3	9.0	0	2.5	55.5	8.3	0.3
4	0-10	65	27	8	100	19.6	5.3	14.4	0.5	4.0	119.0	6.9	0.2
	10-20	65	25	10	100	19.0	5.2	13.6	0.5	1.5	99.0	6.9	0.3
	20-40	60	28	12	100	17.0	5.2	11.6	1.0	2.0	44.5	6.7	0.3
9	0-10	56	36	8	100	26.1	13.0	13.1	0.5	1.5	162.5	6.8	0.2
	10-20	59	34	7	100	20.5	9.8	10.7	0.5	0	75.0	7.0	0.2
	20-40	63	31	6	100	21.3	-	-	0	0.5	30.0	7.2	0.2
7	0-10	55	29	16	100	29.8	8.6	21.2	0	2.5	95.5	6.9	0.3
	10-20	57	22	21	100	22.5	9.0	13.5	0.5	2.0	147.5	7.3	0.3
	20-40	55	20	25	100	20.8	9.1	11.7	0	0.5	58.0	8.4	0.3
11	0-10	52	36	12	100	29.6	8.5	21.1	0	1.0	148.5	7.5	0.2
	10-20	50	39	11	100	26.5	8.1	18.4	0	1.5	101.0	7.9	0.2
	20-40	57	26	17	100	23.3	7.6	15.7	0	2.0	75.5	8.3	0.1
12	0-10	56	32	12	100	27.5	9.0	18.5	0	2.5	150.0	7.5	0.2
	10-20	57	27	16	100	20.3	7.8	12.5	0	2.0	116.5	7.9	0.3
	20-40	64	24	12	100	24.6	9.5	15.1	0.5	0	44.0	8.3	0.3
8	0-10	56	34	10	100	26.6	7.0	19.6	0.5	1.5	162.5	6.8	0.5
	10-20	65	24	11	100	20.8	3.3	17.5	0.5	0	75.0	7.0	0.3
	20-40	67	22	11	100	15.6	3.3	12.3	0	0.5	30.0	7.2	0.1

Stand	Sample Depth (cm)	% Sand	% Silt	% Clay		% Moisture Content -1/3 bars	% Moisture Content -15 bars	Available Moisture Capacity %	N ppm	P ppm	K ppm	pH	Conductivity mmhos
3	0-10	70	18	12	100	18.3	6.0	12.3	0.5	3.0	52.0	6.6	0.3
	10-20	53	28	19	100	22.3	8.8	13.5	1.5	1.0	56.5	6.8	0.3
	20-40	54	28	18	100	24.6	7.6	17.0	0.5	1.0	47.5	6.9	0.3

APPENDIX IV

Means ($\bar{x}$) and Standard Error of Means (S) for soil moisture by volume in stands 2, 5 and 13 over a twelve month period.

Month	10 - 50 cm		25 - 65 cm		40 - 80 cm		55 - 95 cm	
	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s
Oct. 1971	11.9	0.4	11.8	0.7	10.7	0.5	10.6	0.8
Nov.	10.4	1.2	11.2	0.4	10.1	0.5	10.1	0.1
Dec.	12.2	0.7	12.1	0.8	10.7	0.5	9.9	0.7
Jan. 1972	12.0	1.0	10.8	0.7	9.6	0.3	9.5	0.0
Feb.	13.9	1.0	12.1	0.8	11.0	0.6	11.1	0.6
March	14.4	1.3	12.6	0.8	11.1	0.7	12.1	1.2
April	24.0	4.0	17.4	2.0	12.4	1.5	11.0	0.7
May	31.1	1.8	27.0	1.4	20.3	2.7	13.2	0.0
June	26.2	2.4	23.0	2.3	19.3	2.8	16.5	0.0
July	28.8	1.4	22.6	1.8	20.3	3.2	18.1	1.1
Aug.	17.9	1.4	15.8	0.3	14.0	1.4	14.0	0.2
Sept.	17.8	1.3	15.5	1.2	13.7	1.5	13.1	0.3

Month	10 - 50 cm		25 - 65 cm		40 - 80 cm		55 - 95 cm	
	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s
Oct. 1971	11.7	0.8	14.2	2.3	15.1	1.1	19.5	4.6
Nov.	11.6	1.0	12.7	1.3	15.8	2.1	14.9	2.4
Dec.	12.2	1.0	12.9	0.8	14.5	1.2	22.1	6.1
Jan. 1972	11.6	1.1	13.6	1.2	14.4	1.4	18.4	3.7
Feb.	13.2	1.3	16.3	2.7	18.1	2.6	19.9	4.8
March	14.9	1.0	19.0	3.5	19.7	2.7	24.6	1.1
April	18.0	1.0	20.5	2.3	20.6	3.0	19.7	4.2
May	24.2	1.9	25.7	1.9	29.8	1.1	35.2	0.0
June	22.0	1.7	24.2	2.2	26.7	1.4	34.8	2.8
July	23.5	2.3	22.2	1.9	25.5	1.4	35.2	0.0
Aug.	13.0	0.6	14.7	0.8	17.7	1.6	30.0	0.0
Sept.	12.2	0.9	14.0	0.6	16.4	1.8	-	0.0

Month	10 - 50 cm		25 - 55 cm		40 - 80 cm		55 - 95 cm	
	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s
Oct. 1971	18.4	1.1	17.2	0.9	17.9	1.0	19.5	1.6
Nov.	18.0	0.9	17.4	0.9	17.7	0.9	20.3	1.3
Dec.	16.1	0.7	16.0	0.6	17.4	0.8	20.6	1.2
Jan. 1972	16.6	0.5	14.8	0.6	15.9	0.7	18.2	1.2
Feb.	22.7	1.4	17.8	1.7	16.7	0.7	18.5	1.1
March	26.1	1.3	21.3	2.1	18.6	0.7	18.9	0.9
April	31.2	1.8	26.1	2.5	22.0	1.4	20.9	1.3
May	28.1	1.2	26.2	1.8	26.2	1.4	30.7	1.0
June	26.7	1.3	25.6	1.8	26.5	1.9	31.6	2.0
July	25.9	1.1	24.2	1.5	25.8	1.3	30.1	1.9
Aug.	-	-	-	-	-	-	-	-
Sept.	22.2	1.3	-	-	21.8	1.4	26.1	1.9